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THE NORTH AMERICAN GALL MIDGES (DIPTERA: CECIDOMYIIDAE) OF HACKBERRIES (CANNABACEAE: *CELTIS* SPP.)

By

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and
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The North American Gall Midges (Diptera: Cecidomyiidae) of Hackberries (Cannabaceae: *Celtis* spp.)

BY

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ABSTRACT– Twenty-three species of gall midges occur exclusively on hackberries in North America north of Mexico. Twenty-one of them belong to the genus *Celticecis* and form complex, dehiscent galls on leaves and the current year's twigs. *Celticecis* species are definitely known only from the typical subgenus of *Celtis*, distributed through much of the Holarctic Region. Nearctic species do not appear to discriminate among hosts within the subgenus but each has its individual geographic limits. Galls of most species of *Celticecis* grow quickly in early spring, but some have a delayed, late summer development. When full-grown, larvae form cocoons in the galls that subsequently dehisce at various times during summer and autumn. Larvae pupate early the following spring and adults appear shortly after. Some larvae remain in the galls through the entire next year to pupate only in the following spring. Larvae of the second and third (ultimate) instars present some of the best characters for determining species and their affinities. Seven of the ten previously described species of North American *Celticecis* are valid: *Celticecis capsularis* (Patton) (= *Celticecis painteri* (Felt), **new synonym**), *Celticecis celtiphyllia* (Felt), *Celticecis oviformis* (Patton), *Celticecis pubescens* (Patton) (= *Celticecis texana* (Felt), **new synonym**), *Celticecis semenrumicis* (Patton), *Celticecis spiniformis* (Patton (= *Celticecis unguicula* (Beutenmüller), **new synonym**), and *Celticecis wellsi* (Wells). Fourteen **new species** of *Celticecis* are named and described: *Celticecis aciculata* Gagné, *Celticecis acuminata* Gagné, *Celticecis conica* Gagné, *Celticecis connata* Gagné, *Celticecis cornuata* Gagné, *Celticecis cupiformis* Gagné, *Celticecis expulsa* Gagné, *Celticecis globosa* Gagné, *Celticecis ovata* Gagné, *Celticecis pilosa* Gagné, *Celticecis pyriformis* Gagné, *Celticecis ramicola* Gagné, *Celticecis subulata* Gagné, and *Celticecis supina* Gagné. *Celticecis* is to date known also from the Japanese *Celticecis japonica* and an undescribed species from Turkey. *Peracecis* Gagné, **new genus** is described for a **new species**, *P. fugitiva* Gagné, responsible for an integral leaf gall found in southern U.S. *Parallelodiplosis acernea* (Felt), a widespread inquiline in cecidomyiid and psyllid galls of hackberry, is redescribed and compared to its congeners. Keys to galls and larvae (second and third instars) of Nearctic gall midges on hackberry are presented. Other cecidomyiid galls previously reported on *Celtis* outside North America are noted.

INTRODUCTION

North American hackberries (*Celtis* spp.) are host to a great variety of insects and mites. Gall makers of hackberries, comprising mainly psyllids (Hemiptera: Psyllidae) and gall midges, are a large component of this fauna (Riley 1890; Felt 1940, 1965). While psyllids form the more conspicuous galls of hackberries and are often regarded as pests, the gall midges have generally been ignored because their galls are less conspicuous.

Before this study little was known about hackberry gall midges. Eleven North American species had been named but only sketchily described. Ten of them belonged to *Celticecis* and were known from various leaf and stem galls on hackberries in the eastern half of the United States. Their identities were uncertain because five species were based only on galls and a few others had been described without their authors having taken previously named species into account. The eleventh species was *Parallelodiplosis acernea* (Felt), a fatal inquiline in galls of both cecidomyiids and psyllids on hackberries in New York (Moser 1965). Outside of North America, one named species of *Celticecis* was known from hackberry leaf galls in Japan (Yukawa & Tsuda 1987), two galls from Japan attributable to *Celticecis* were mentioned in Moser (1965), and we knew of an undescribed species from Turkey (Gagné & Moser 1997).

By treating in a comprehensive way the gall midges of hackberries of North America we hoped to uncover the whole suite of hackberry gall midges in the Nearctic Region and determine their host specificity, geographic distribution and placement within the context of other Cecidomyiidae. Our results confirm that a simultaneous examination of all of the gall midges on a particular host genus is the most effective way to study phytophagous gall midges. We describe or redescribe here 23 North American species. Names are provided for new species and a new genus, and relationships among the taxa are determined based on morphology. A molecular analysis in preparation by Scheffer *et al.* appears to support the relationships reported in this paper. We confirm the generalization of Gagné (2008) that more species of phytophagous gall midges occur where their host genus is most common, widely dispersed and most speciose and, alternatively, that fewer species occur where the host range is fragmented.

HISTORY

The first published mention of cecidomyiid galls on hackberries was by Charles V. Riley (1890) in a general article on insects injurious to these trees. Among the many insects he listed, he differentiated six "of the more striking galls" caused by cecidomyiids. He wrote that he made no attempt to describe "the insects which make them and which are very difficult to rear." No illustrations of these galls accompanied the paper but his written characterizations allow one to identify the galls with a high degree of confidence. In addition, samples of the galls he collected in Missouri and Texas were deposited in the National Museum of Natural History in Washington, DC, where they still reside.

Shortly afterwards, William H. Patton (1897), an amateur entomologist from Connecticut who had worked as an assistant to Riley during 1880 and 1881 in Washington, D.C. (Britton & Howard 1921), wrote a short publication illustrating a scheme for naming galls before the gall makers could become known by subsequent rearing. He coined the generic name from an already existing genus-group name and combined that by a hyphen to the genitive form of the host's name. The result in this case was *Cecidomyia-celtis*. He then gave the gall itself a specific descriptive name, as in his type species *deserta*, named for hollow, elongate swellings of hackberry twigs. To exemplify the principle further, he gave specific names to five of the six cecidomyiid leaf galls described by Riley (1890), namely *C.-c.* [*Cecidomyia-celtis*] *oviformis* Patton, *C.-c. semenrumicis* Patton, *C.-c. pubescens* Patton, *C.-c. capsularis* Patton and *C.-c. spiniformis* Patton. Although founded on the galls alone, the species names are valid because they were based on the work of an animal and proposed prior to 1931 (Art. 1.2.1 in *International Code of Zoological Nomenclature* 1999). The gall former for the type species was subsequently found to belong to Agromyzidae (Diptera) (Gagné 1983). *Cecidomyiaceltis* is itself an unavailable name (Art. 1.3.7 in *International Code of Zoological Nomenclature* 1999).

William Beutenmüller, an entomologist at the American Museum of Natural History in New

York, described a sixth species, *Cecidomyia unguicula* Beutenmüller (1907), from adults reared in Ohio by B.W. Wells (of whom more to follow). Beutenmüller's species is treated as a synonym of *C. spiniformis* in this paper.

Ephraim P. Felt of the New York State Museum in Albany and important pioneer in the study of gall midges (Gagné 1994) named the seventh through tenth species of gall makers from hackberries: *Mayetiola celtiphyllia* from Iowa (Felt 1908), *Phytophaga wellsi* Felt (1916) (now *Celticecis wellsi* (Wells)) from Ohio, and *Phytophaga painteri* and *Phytophaga texana* from Texas (Felt 1935). Felt described these species from adults sent to him by correspondents and may not have seen the galls firsthand. The last two of the four species are treated here as junior synonyms of two of Patton's species.

Bertram W. Wells, a professor of botany at Ohio State University, was interested in gall structure. One particular paper on the anatomy of hackberry galls made by various insects and mites included detailed drawings, whole and in section, of nine distinct kinds of cecidomyiid galls known to him from Ohio and possibly Kansas (Wells 1916). Pertinent plates from his paper are reproduced here (Plates 1–2) because they treat the gall structure of several species in much more detail than we do. Wells considered the five Patton species invalid, based as they were on only the work of the insects. He attached only three names to particular galls, viz., *C. unguicola* [sic!], *P. celtiphyllia* and *P. wellsi*. Wells (1916) anticipated Felt's description of *P. wellsi* by using the scientific name for the gall before Felt's paper appeared later in the same year. The result is that *P. wellsi* is attributed to Wells and not to Felt.

One of us, JCM, began in the 1950s an inquiry into the gall makers of hackberry and their parasitoids that resulted in a synopsis of world hackberries with preliminary studies of psyllid and cecidomyiid galls (Moser 1954). He initiated the study of hackberry gall midge larvae by drawing outlines of their spatulas, the dermal thoracic structures characteristic of most third instar and sometimes even second instar cecidomyiid larvae, from several species available to him. This work was later followed by a more in-depth study on the interrelationships of three hackberry gall makers, two of them psyllids, the other the cecidomyiid *C. spiniformis* (as *Phytophaga* sp. near *spiniformis*) and their natural enemies (Moser 1965). A fatal inquiline, *Parallelodiplosis acernea* (Felt), was discovered in galls of both the gall midge and psyllids. That cecidomyiid was until then known from a single male caught in flight.

Gagné (1983) gathered the ten known gall midge species of hackberry into the new genus *Celticecis* based on evident similarities. He later treated the galls caused by nine of the ten species in *The Plant-Feeding Gall Midges of North America* (Gagné 1989).

Celticecis was presumed to occur in Japan since Moser (1965) reported galls that were probably attributable to cecidomyiids. That *Celticecis* occurs outside of North America was confirmed by Yukawa & Tsuda (1987) with their description of *Celticecis japonica* from southern Japan. Two other species have more recently been found in Japan (Sato & Yukawa, in preparation), indicating that *Celticecis* should be found even more extensively in the Far East. The genus is as yet unknown in Europe, but Gagné & Moser (1997) reported a *Celticecis* from Turkey, the first documentation of the genus from Eurasia outside of Japan.

THE HACKBERRIES

Celtis comprises some 60 species of shrubs and trees of temperate and tropical regions of the World (Sherman-Broyles *et al.* 1997). The genus was already present and widely represented in North and South America and eastern Asia during the Paleocene Epoch 64–56 million years ago (Manchester *et al.* 2002). Seven species occur presently in North America north of Mexico. Five of them, listed in the accompanying Table 1, belong to the subgenus *Celtis*, which is host to all the North American cecidomyiid galls that we found. The other two North American species are *Celtis* (*Mertensia*) *iguanaea* (Jacq.) Sarg., the iguana hackberry, and *Celtis* (*Mertensia*) *pallida* Torr., the spiny or desert hackberry. Both reach only into very southern United States but their ranges extend south to Argentina. Two other species from the Americas belong to the subgenus *Celtis*. These are *Celtis jamaicensis* Planch., endemic to Jamaica, and *Celtis caudata* Planch. which occurs from northern Mexico south to Nicaragua. Specimens of these

Table 1. Scientific and common names of *Celtis* (*Celtis*) species of North America north of Mexico.

Celtis laevigata Willd.	sugarberry
Celtis lindheimeri Englem. ex K. Koch	Lindheimer hackberry
Celtis occidentalis L.	northern hackberry
Celtis reticulata Torr.	netleaf hackberry
Celtis tenuifolia Nutt.	dwarf hackberry

two species in the National Museum of Natural History botanical collection were examined for galls but no galls or possible signs of attachment were found.

Northern hackberry and sugarberry are the most wide-ranging species in eastern North America (Map A) and were the hosts from which we collected most of our study material. Northern hackberry occurs in the northeastern quadrant of the United States and into southern Ontario and Quebec. It is much more common in midwestern than in eastern U.S. It overlaps on its southern margins with sugarberry, the common hackberry of the SE quadrant of the United States. Sugarberry has also a spotty distribution in northern Mexico that is not shown on Map A. The remaining three species of hackberry in the U.S. are uncommon or sporadic. The usually shrubby dwarf hackberry can be found in the eastern half of the U.S., sometimes alongside northern hackberry and sugarberry, but is nowhere as common. Lindheimer hackberry is a tree or shrub that grows discontinuously in southcentral Texas and northern Mexico. Netleaf hackberry is the only native farwestern North American species of *Celtis*. It extends sporadically north and west from Louisiana and Texas to Washington and California.

Hackberries in Japan and Turkey with known *Celticecis* galls also belong to the subgenus *Celtis*. See under "Gall midges on *Celtis* reported outside North America" for notes on those species and their galls.

MATERIALS AND METHODS

Host names.—Common names for Nearctic hackberries are used in the text except in the introduction and Table 1. This will avoid confusion that might occur in using the abbreviation "*C.*" for both *Celtis* and *Celticecis*. The names hackberry and hackberries will refer to the genus *Celtis*, while northern hackberry will specify *Celtis occidentalis* and sugarberry, *Celtis laevigata*.

Names of gall midges.—New species names are all Latin and refer to some aspect of the gall. Table 2 lists the species we treat here that are found on hackberries in North America north of Mexico. The list also suggests common names for future use. The taxonomic and descriptive parts of this paper were the responsibility of RJG, the author of the new species.

Collections.—Most galls and their cecidomyiids used for this study were collected by us since the summer of 2008. JCM regularly collected each week in Alexandria, Louisiana from April to October of the 2010 and 2011 seasons to survey the progression of the galls from first appearance to maturity and eventual dehiscence. Galls were collected by RJG throughout the season in Maryland and eastern West Virginia, but not so regularly from any one locality because galls were scarcer there. RJG also collected during this period from hackberries in Florida, Mississippi, Louisiana and Texas, and on three separate trips to Ohio and Kentucky. In addition, many colleagues whose names are listed in Acknowledgments kindly collected or reported galls from various places. Historic material, including types, was available from the National Museum of Natural History, Washington, D.C. (USNM), the American Museum of Natural History in New York (AMNH), and the Felt Collection. The last is the property of the New York State Museum in Albany (NYSM) but is currently on loan to the Systematic Entomology Laboratory in Washington, D.C.

Gall-bearing leaves and other plant parts were removed from trees and placed in a plastic bag with collection data. Galls from JCM and others were sent to RJG by various carriers. No apparent ill effect came to the galls for being in the mail for the usual transit period of 2 to 4 days. Examination of the galls was made with the aid of a dissecting microscope. Representative galls were cut open and cecidomyiid larvae removed and preserved in alcohol. Samples of whole and cross-sectioned galls were glued to a card, then pinned and labeled with collection data for permanent reference. Larval samples were placed in 70% alcohol and labeled, some to be slide mounted or

Map A. Native distribution of northern hackberry (upper outline) and sugarberry (lower outline). Redrawn from Little (1971).

Table 2. List of gall midges (exclusive of *Lestodiplosis* sp.) on hackberries in North America north of Mexico, with suggested common names for their galls.

Celticecis aciculata Gagné	hackberry aciculate gall
Celticecis acuminata Gagné	hackberry narrow-tipped gall
Celticecis capsularis (Patton)	hackberry rosette gall
Celticecis celtiphyllia (Felt)	hackberry acorn gall
Celticecis conica Gagné	hackberry jelly bean gall
Celticecis connata Gagné	hackberry aggregate gall
Celticecis cornuata Gagné	hackberry horn gall
Celticecis cupiformis Gagné	hackberry barrel gall
Celticecis expulsa Gagné	hackberry popout gall
Celticecis globosa Gagné	hackberry globular leaf gall
Celticecis ovata Gagné	hackberry tenpin gall
Celticecis oviformis (Patton)	hackberry spherical stem gall
Celticecis pilosa Gagné	hackberry fuzzy cone gall
Celticecis pubescens (Patton)	hackberry pubescent gall
Celticecis pyriformis Gagné	hackberry pear-shaped gall
Celticecis ramicola Gagné	hackberry columnar stem gall
Celticecis semenrumicis (Patton)	hackberry winged gall
Celticecis spiniformis (Patton)	hackberry thorn gall
Celticecis subulata Gagné	hackberry awl-shaped gall
Celticecis supina Gagné	hackberry recumbent gall
Celticecis wellsi (Wells)	hackberry top-shaped gall
Parallelodiplosis acernea (Felt)	hackberry inquiline gall midge
Peracecis fugitiva Gagné	hackberry blister gall

used for SEMs, some for the permanent collection. Other larvae were kept in 95% alcohol in a freezer for later molecular analysis.

Adult rearing.—Samples of galls still on leaves were cut open throughout the growing season to determine when the larvae spun their cocoons. Depending on when larvae of each species had achieved this stage, unopened galls were segregated by kind and placed in pots of approximately 7 cm in each dimension and filled with dampened peat moss. The peat moss, used because its acidic nature prevents most fungal growth, had first been cooked in a microwave oven to kill any mites or insects. Each pot was placed in a clear, gallon-size plastic bag, its open end rolled and knotted closed, and kept at room temperature out of direct sunlight. In November the pots were taken out of the plastic bags, watered and placed in a refrigerator at a temperature just above freezing. Care was taken not to allow the pots to become dry while in the refrigerator. At the end of February the pots were freshly watered and placed in new individual plastic bags, their ends rolled and knotted, and kept at room temperature. In due course adults of gall midges and hymenopterous parasitoids emerged from some of the galls or from the peat moss itself, as did *Peracecis fugitiva* and some *Parallelodiplosis acernea*. The plastic bags were checked daily for adult emergence. Adults were removed from the bags by catching them with an artist's brush dipped in alcohol and transferring them to a vial of 70% alcohol. Following emergence, pupal exuviae could be seen sticking out of the galls or surface of the peat moss and were easily harvested. After a sufficiency of adults emerged, galls were cut open to retrieve whole pupae to use for scanning electron micrographs (SEMs). It is important to have many galls in a rearing pot, at least 50 or more of each kind, because of the high mortality rate of the larvae. Cutting open galls in advance of spring is fatal to any *Celticecis* inside, so one cannot be certain beforehand of the

state of the larvae, whether they are parasitized or already dead from other causes. Adults of some of the less common species treated here were not reared because their galls were never found in sufficiently large numbers or at the proper time. Most reared adults were kept in 70% ethyl alcohol for eventual slide mounting or re-drying for SEM viewing. Parasitoids that emerged with gall midges were saved in 70% alcohol, identified by colleagues, and are now housed in the Hymenoptera collection in the USNM.

JCM and R. Fitzgibbon found some adult gall midges flying among burgeoning hackberry buds and new leaves in spring. While some of these proved to belong to *Celticecis*, they could not be identified to species because that stage generally lacks reliable distinguishing characters. As a rule, sweeping or otherwise trapping adults of phytophagous cecidomyiids in flight is not a useful endeavor. In addition, associating both sexes of plant-feeding gall midges is usually not verifiable unless they are reared from similar galls. Slide mounting, a requirement for studying these insects, is a time-consuming activity better spent on reared samples.

Specimens examined and their preparation.—Most of the larvae and adults examined during this study can be traced to particular galls or gall lots that are either mounted on pinned cards or kept in alcohol. Holotypes of new species and most other specimens used in this study are deposited in the insect collection of the USNM.

Most larvae used for microscopic study were mounted in Berlese's medium by JCM using the following procedure: Specimens were taken from 70% alcohol and placed in deep well slides containing lactophenol that were placed in a drying oven for about four hours to allow adequate clearing. A small drop of Berlese's medium was then placed in the center of a microscope slide. Each larva was placed in this medium and arranged dorsoventrally so that all important morphological structures could be clearly seen. A 12 mm diameter cover slip was then lowered over the medium and pressed down to flatten the specimen. The slide was placed in an oven overnight to harden the medium. When dry, the slide was placed on a slide ringer that was spun so that a small amount of electrical paint could be brushed around the cover slip to seal the preparation. The slide was then placed in an oven for about five hours to dry. Adults, pupal exuviae and some additional larvae were mounted in Canada balsam following the technique outlined in Gagné (1989, 1994).

SEMs are ideal for illustrating the anterior segments of whole pupae. If possible the same specimen was rotated to take photos of both ventral and lateral aspects of the anterior segments. Pupal exuviae mounted on slides are by contrast often distorted, especially anteriorly, where the antennae and occiput can become partially disconnected from the remainder of the body after eclosion.

Descriptions.—In the species descriptions, the gall appears first because it is the most obvious manifestation of a species. Gall descriptions give information about location on the host, whether galls are single or gregarious, their external shape, texture and color, dimensions, connection to the host, wall structure in longitudinal section, and shape of the larval chamber. All galls in Figs. 1–54 are shown with apices upwards, even though most leaf galls are found in nature apex downwards on the lower surface of the leaves. Those in Plates 1–2 from Wells (1916) were drawn with their apices downwards.

Some species are named and described here on the basis of only the gall and larva because during the period of this study we did not succeed in rearing adults. In a comprehensive study the absence of adults of some species should not preclude describing species from larvae alone. These have some of the best distinguishing characters, their hosts and distributions are known, and their characteristic galls can be found again, possibly to successfully rear adults at some future time

Distribution lists, maps and specimen localities.—The distribution list for each species is given alphabetically by state and county or town. The maps show each of these occurrences for the plant feeding species. Voucher specimens for the gall records are deposited in the USNM, either pinned or in alcohol. Listed also, with citations, are galls from publications, e.g., Sears (1914), when accompanied by identifiable illustrations. A separate list of larvae, pupae, and adults of each species studied gives the collection and rearing (if any) data in alphabetical order by state or province, and town or other site, followed by collection date, collector, and life stage. Collector abbreviations RJG and JCM stand for R. J. Gagné and J. C. Moser,

respectively. All the specimens used in this study, except some types and records from publications or photographs, are deposited in the USNM.

Species concept within *Celticecis*.—We considered a distinct gall the phenotypic extension of a discrete species. By "distinct" we mean fully-developed galls because young, growing galls of many species may be mistaken for those of other species. The reason for this is that *Celticecis* galls grow to their full length before filling out laterally. Gall variation in certain species also requires a little experience from a viewer, which is why more than one gall is illustrated here for some species.

GENUS *CELTICECIS* GAGNÉ

Celticecis Gagné 1983: 436. Type species, *Mayetiola celtiphyllia* Felt, by original designation. Gagné 2004, 2010 (catalog).

Diagnosis.—*Celticecis* is assigned to the cecidomyiine supertribe Lasiopteridi on the basis of the following combination of characters: an irregular number of antennal flagellomeres, the single node with unlooped circumfila of the male flagellomeres, the lack of a dorsal occipital protuberance, the presence of gonocoxal lobes sheathing the aedeagus, and the presence of setae on the ventral papillae of the larval eighth abdominal segment. Adult *Celticecis* spp. can be characterized by the lack of a separation in the costal wing vein at its juncture with R_5, the untoothed claws in at least the Nearctic species, the gonocoxal lobe sheathing the aedeagus not subdivided ventrally and dorsally. Larvae have a reduced spatula in the third instar, have lost at least two of the primitive six papillae on each side of the spatula, and the second instar also has a sternal spatula in all except one species. All species are found in complex galls on the leaves, twigs and fruit of *Celtis* (*Celtis*) and pupate inside the gall. Adults are similar to those of the new genus *Peracecis* in some ways, particularly in the undivided gonocoxal lobe sheathing the aedeagus and the lack of a separation in the costal wing vein at its juncture with R_5. Both characters are rare for Lasiopteridi. The tarsal claws of the two genera are different, those of *Celticecis* simple, those of *Peracecis* toothed. The larval stage of *Celticecis* has a spatula in the second instar (except for *C. cornuata*), a reduced spatula shaft in the third instar, and only 2–4 lateral papillae on each side, while *Peracecis* (q.v.) has retained the primitive alternative states common to those taxa that leave the gall to pupate in the soil.

Description.—*Adult*. Color: Body dusky, extensively covered with dark scales. **Head** (Figs. 55–56): Eyes connate at vertex; facets circular and closely adjacent except slightly farther apart anterolaterally. Occiput evenly convex, without dorsal protuberance, covered with scales. Frons with extensive mixed setae and scales. Labrum triangular. Labella separate, well-developed, covered with short, stout setae laterally. Palpus usually 4-segmented, occasionally a segment missing in species of reduced size, with scattered setae and scales. Antenna with cylindrical scape with a few scales on venter, a shorter, spheroidal pedicel with row or rows of scales chiefly on venter, and 10–23 flagellomeres; flagellomeres progressively narrower and shorter towards antennal apex. Male flagellomeres each with large node and, except for ultimate flagellomere, a naked distal neck of variable length; the nodes with basal circumfilum connecting to one other that arches around the ventral limits of the node; setae basad of basal circumfilum straight, more numerous and shorter ventrally than dorsally; setae covering most of venter above basal circumfilum retrorse with bulging bases; additionally a few scattered setae elsewhere on dorsum; remainder of surface covered with setulae. Female flagellomeres barrel-shaped, without necks, the nodes usually surrounded by two horizontal circumfila joined by two vertical but occasionally irregular connective fila; vestiture essentially as in male except retrorse setae not as long. **Thorax**: Scutum with 2 dorsocentral and 2 lateral rows of setae with some scales intermixed. Scutellum with setae and a few scales dorsally but discontinuous mesally. Anepisternum with scales on dorsal half; anepimeron mostly covered with setae with a few scales intermixed; pleura otherwise naked. Wing: widest near mid-length, surface covered with scales: Rs absent; R_5 nearly straight except slightly curved apically, joining C near wing apex; C unbroken at juncture with R_5; M_3 evanescent; Cu forked. Legs covered with scales and and a few setae, the setae often in distinct rows; tarsal claws (Figs. 57, 121–122) untoothed, evenly curved near mid-length; empodia approximately as long as claws; pulvilli ca. 1/3 length of claws. **Male abdomen**: First through seventh tergites entire, rectangular, ca. 2× as wide as long; all with anterior pair

of trichoid sensilla, row or rows of setae along posterior margin, and covered with scales; lateral setae absent except in *C. japonica* with lateral setae present on third through seventh tergites and in *C. celtiphyllia* with lateral setae present only on seventh tergite; eighth tergite less pigmented posteromesally than elsewhere, with pair of anterior trichoid sensilla, several scattered posterior setae with or without scattered scales intermixed. Second through eighth sternites ca. as wide as long, each with closely approximated anterior pair of trichoid sensilla, rows of setae mixed with scales along posterior margin, an irregular horizontal row of setae at mid-length and with scales on anterior half. Terminalia (Figs. 58–61, 119–120, 123): cerci ovoid, with apical and subapical setae; hypoproct deeply incised, resulting in two elongate cylindrical lobes, each with a few setae apically, evenly setulose dorsally and ventrally; gonocoxite laterally elongate-cylindrical, medially with undivided lobe subtending one side of aedeagus, lobe covered with setulae and with apical group of short setae on raised bases; gonostylus tapering from broad base to apex (Fig. 119) or widest near mid-length (Fig. 123); aedeagus bare, broad, apically flattened dorsoventrally, the distal lip curved dorsally; basal apodeme keel-like. **Female abdomen** (Figs. 62–70, 124–127): First through sixth tergites entire, rectangular, vestiture generally as in male with the following exceptions: lateral setae present on tergites 3–7 only on *C. japonica*; posterior setae absent medially and scales almost entirely absent on *C. oviformis*. Seventh tergite rectangular, appreciably narrower than sixth tergite, with several rows of setae along posterior margin, with variable scale covering and anterior pair of trichoid sensilla; pair of pseudosclerites present between seventh and eighth tergites, easily visible in well-pigmented specimens, these structures not always continuous with seventh tergite; eighth tergite entire (Fig. 127), of same general shape as seventh tergite, to appreciably longer than preceding tergite (Figs. 124–126) and partially or completely divided longitudinally into two sclerites each with an anterior trichoid sensillum and short scattered setae along posterior margin. Sternites with vestiture as for male, not pigmented and with only a few scales on much of posterior half anterior to posterior setae; second through sixth sternites ca. 2× as wide as long, seventh slightly longer than and half the width of sixth, eighth sternite not apparent. Ovipositor barely protrusible with bulbous fused cerci in *C. japonica* (Figs. 62–65), or variably elongate with fused cerci cylindrical and approximately 1, 2 or 3 times as long as high (Figs. 66–70); ninth segment cylindrical, of subequal diameter throughout, with conspicuous pair of sclerites extending laterally from base to cerci (Figs. 124, 127).

Pupa (Figs. 71–72). Integument unpigmented except at apices of antennal bases. Vertex convex, on each side anterolaterally with long seta situated on conspicuous convexity. Antennal bases variously shaped, usually closely approximated and acutely angled ventroapically. Face convex and either completely smooth or with protuberance at mid-length on each side; with more or less conspicuous triplet of papillae near base of each palpus, one of them setose. Frons with or without short- to long-setose papillae. Prothoracic spiracles elongate, tapered to pointed apex. Abdominal tergites, pleura and sterna evenly spiculose, the spicules slightly longer and closer together on tergites than elsewhere; tergites with horizontal row of 6 setose papillae.

Larva. **Third instar** (Figs. 95–98): White, yellow or orange. Generally spindle-form, cylindrical to slightly flattened dorsoventrally, more or less sulcate intersegmentally. Head directed anteriorly, hemispherical, antennae ca. 2× as long as basal width, posterolateral apodemes as long as head capsule. Spatula usually robust though short, with 2 triangular, acute anterior teeth and more or less quadrate shaft, with tooth single in some northern specimens of *C. spiniformis* (Fig. 146), or vestigial in *C. capsularis* (Fig. 130) and *C. cupiformis* (Fig. 131). Body almost entirely covered with rounded verrucae. Papillae as follows: usually only 2 ventrals apparent on collar segment; dorsals 4–6 except eighth segment with 2; pleurals 1–2 per side, all with setae; terminals 4–8, all with setae; sternals 2 on thoracic segments, 2–4 on first through seventh abdominal segments, without setae except in *C. cornuata* and *C. japonica*; 2–4 laterals on each side of ventral midline of thoracic segments, their setae prominent, shorter than width of papillar bases, or not apparent; ventrals 1 on each side of thoracic segments and first through seventh abdominal segments, each with seta, 1–2 on each side of eighth abdominal segment, with or without setae; anal papillae usually not apparent, occasionally 1–2 present each side of anus. **Second instar** (only characters differing from third instar): Flattened spindle-form. Spatula

present except in *C. cornuata*, usually with single (occasionally 2), triangular, acute anterior tooth and circular to quadrate, occasionally lobed shaft. Body mostly covered with acute spinules. **First instar**: White to translucent. Flattened cylindrical, terminal segment broadly rounded. Head capsule without apodemes. Antenna elongate, 4 times as long as basal width. Spiracles present only on prothorax and eighth abdominal segment, pointed on prothorax, larger, circular and blunt on eighth segment. Body mostly smooth, with fine spicules anteroventrally on abdominal segments and covering terminal segment.

Egg. Sausage-shaped, rounded at both ends, in *C. celtiphyllia* ca. 0.14 mm long by 0.04 mm wide.

Intrageneric Morphology and Relationships

The fact that 90 million years ago hackberries were recognizable and already distributed across the Holarctic Region (Manchester *et al.* 2002) gives *Celticecis* a hypothetically long ago platform on which to evolve and helps explain its present Holarctic-wide distribution. *Celticecis* is restricted to hackberries in complex, dehiscent galls but is otherwise diverse in many ways. Shared, derived, not necessarily unique character states of the genus are the lack of a break in the costal wing vein immediately beyond its junction with R_5, the lack of basal teeth on the tarsal claws, the undivided gonocoxal medial lobe, the presence of a pseudosclerite between the female seventh and eighth abdominal tergites, and the presence of several secondary characters in the larvae, mainly the modified spatula, successive losses of papillae, and, in all but one species, the presence of a spatula in the second instar. These and other character states that are not necessarily unique to *Celticecis* are outlined in turn below, as are realizations and recommendations about various characters for work on other genera.

Within *Celticecis* the number of antennal flagellomeres varies but seems correlated with the size of a species. The longer the wing, used as an index of body size, the greater the number of flagellomeres. It should be noted that antennae of Cecidomyiinae have more sensilla on the ventral surface, which is the leading edge of the antennae during flight. It is important in illustrating flagellomeres to show at least the ventral surface and preferably both. If only one side is drawn, the illustration should be labeled as to the surface shown (cf. Figs. 115–118).

The costal vein of wings of Cecidomyiidae is most often broken just past its juncture with R_5 but is joined in *Celticecis*. The lack of a break is not unique within Lasiopteridi (Gagné 2009), and in the supertribe Cecidomyiidi it is unbroken also in *Thecodiplosis* (Kieffer 1895, Harris 1966) and *Caryomyia* (Gagné 2008). Nevertheless, a break or lack thereof is a practical generic key character. Inasmuch as C is broken just beyond R_5 in most cecidomyiids, including Lestremiinae and Porricondylinae, one supposes that the lack of a break in some Lasiopteridi where *Celticecis* belongs, as well as in a few Cecidomyiidi, is a derived character state. Several other genera of Lasiopteridi also have no break in the costa (e.g., *Acericecis*, *Semudobia*, *Psectrosema*), but major differences between these genera and *Celticecis* and among each other indicate that this lack of a break evolved more than once.

The presence or absence of lateral setae midway between the anterior and posterior margins of the abdominal tergites has also been used as a good key character in Lasiopteridi (Gagné 1981, 2008). Their presence is presumably the primitive condition. While absent in most *Celticecis* spp., lateral setae are found on the tergites of both sexes of one species, *C. japonica*, and are retained on only the male seventh tergite of *C. celtiphyllia*.

The presence or absence of scales on the abdominal tergites can also be a useful character for separating genera (Gagné 1981). In *Celticecis* abdominal tergal scales are present on all but females of *C. oviformis*. Males of *C. oviformis* are unknown.

One character found in females of this genus may not be unique but seems worthy of comment. Extending partially or entirely between the seventh and eighth tergites in well-sclerotized specimens of species with elongate ovipositors are two longitudinal pseudosclerites. These are visible in Figs. 125 and 126 as two separate sclerites, but in Figs. 124 and 127 as definite posterior extensions of the seventh tergite. These tergal extensions possibly give additional support to a long ovipositor and for now can be considered an apomorphy in this genus.

The length of the ovipositor in *Celticecis* ranges from barely protrusible in *C. japonica* (Figs. 62–65) to elongate, with consequent lengthening and complete longitudinal division of the eighth ter-

gite in *C. celtiphyllia* and *C. expulsa* (Figs. 66, 124). The fused cerci are broad and bulbous in *C. japonica* but cylindrical and variably short to long in the remaining species. A short ovipositor is the most likely primitive condition because once an ovipositor elongates, with attendant changes in the sclerites and organ systems, reversibility in all of these separate parts and organs would seem unlikely. The length of the cerci in connection with the shape of the eighth tergites is an effective character here for sorting species into groups.

The female ninth segment, the stiffer half of the ovipositor beyond the eversible extended eighth segment, bears a conspicuous, thin lateral sclerite along each side (Fig. 70). These sclerites are not visible in slide mounts of *C. japonica* but one is evident in the SEM (Fig. 62). These sclerites are widespread among Cecidomyiinae and evidently serve to stiffen the ovipositor (Gagné 2009). It now appears from present unpublished observations by RJG that these sclerites have developed in different ways. For example, in *Celticecis* they are uniformly hard and thin, whereas in *Dasineura* and *Rabdophaga* they are on each side somewhat wider and subdivided by closely placed, oblique, parallel lines. These stuctures possibly serve to allow the ninth segment in those genera to inflate during oviposition. Their presence or absence should be part of a description so that we may eventually document more fully the taxonomic distribution of this attribute.

The male terminalia are in most aspects remarkably uniform in *Celticecis*. Those of only *C. connata* and *C. expulsa* differ appreciably from the others. In those two species, gonostyli are largest near mid-length and taper abruptly to the apex (Fig. 61); in all others the gonostyli are largest near the base and taper gradually toward the apex (Figs. 58–60).

Pupal antennal bases, often called "pupal horns," are useful for species recognition in many phytophagous genera, as they are here to a certain extent, although in *Celticecis* they do not attain the size or complexity of some other genera. The reason for this may be that the apices of *Celticecis* galls are not hard and tend to break off easily even before the galls have spent the winter in the leaf litter. In most species of *Celticecis*, the antennal bases are pyramidal, have a keel-like ventral edge and are for most of their length closely adjacent (e.g., Figs. 75–76). Two species stand out as different from the norm. In *C. celtiphyllia* the apices are wide apart (Fig. 73) and in *C. globosa* the antennal bases are dorsoventrally flattened and leaf-like (Figs. 87-88). A few species have facial protuberances, but they may not always be present in at least *C. celtiphyllia*. They are regularly present in *C. capsularis* (Figs. 79–80), *C. connata* and *C. expulsa*. Inasmuch as *C. capsularis* seems more closely related to *C. spiniformis* than to the other species that have these protuberances, these structures appear to have developed independently in the genus.

Celticecis primitively has the full complement of larval papillae for the subfamily except for the loss of two or more laterals on each side of the midline of the thoracic segments. Within the genus other papillae or their setae are lost individually and sequentially, including in some the loss of all or some ventral papillae of the eighth abdominal segment. This last is unusual for the supertribe Lasiopteridi because setose ventral papillae on the eighth abdominal segment are otherwise a defining character of this supertribe. This loss in Lasiopteridi is seen elsewhere only in *Novocalmonia*, a genus with no other resemblance to *Celticecis* (Gagné & Etienne 2009). Also concerning papillae, sternal papillae are only rarely found with setae in Cecidomyiinae. In this genus they are found in both *C. japonica* and *C. cornuata* but this happenstance is not necessarily synapomorphic because no other characters appear particularly to join this pair of species.

The third instar spatula of *Celticecis* is usually short and broad but has secondarily almost disappeared in *C. capsularis* and *C. cupiformis*. The spatula of *C. cornuata* is the only one in the genus that suggests a more plesiomorphic spatula. It is a little longer and its teeth are closer together than in congeners, bringing its shape closer to the clove-shaped spatula primitive for Lasiopteridi.

That the second instar of most *Celticecis* has a spatula is one more example of an uncommon phenomenon that evidently occurs anew in unrelated genera where, presumably, it acts as a scraper inside the galls. Gagné (2008) listed examples of unrelated genera with a second instar spatula. It is absent in *Celticecis* only in *C. cornuata* and it is not possible to say whether one never developed in that species or was secondarily lost. A second instar character that helps define a cluster of species (see under *C. spiniformis*) is the size of the ventral spicules on each side of the midline. In this group these spicules are enlarged and appreciably larger

than the spicules elsewhere on the body. The species of this group, with the exception of *C. supina*, form galls on the leaf lamina. All other species of *Celticecis* outside this group near *C. spiniformis* form galls on veins, petioles, stems, or fruit.

Affinities

Celticecis and *Peracecis* appear generally similar in the adult stage. In particular they share similarly shaped abdominal tergites and sternites, including the pair of long, pigmented and undivided lateral sclerites of the female ninth abdominal segment, an undivided gonocoxal lobe sheathing the aedeagus, and an unbroken costal vein at its juncture with R_5. One difference between the two genera is that at least North American *Celticecis* species have simple tarsal claws while *Peracecis* has toothed claws. This difference should not be weighed highly inasmuch as some genera of Lasiopteridi, e.g., *Rabdophaga* and *Mayetiola*, include some species with toothed and some with simple claws. Larvae of *Celticecis* and *Peracecis* are distinctly different, with those of *Celticecis* having undergone changes in the shape of the spatula, the development *de novo* of a second instar spatula, and various losses of papillae, all of which can be ascribed to life in complex galls (Gagné 2008, Gagné & Waring 1990). By contrast, larvae of *P. fugitiva* that live in a simple pouch gall from which they escape to pupate in the soil have a clove-shaped third instar spatula, no second instar spatula, and the full complement of papillae for Lasiopteridi. Interestingly, this situation is homologous to two genera that occur on *Carya* and also appear to be related to one another. The many species of *Caryomyia* form complex galls in which larvae pupate, while the two species of *Caryadiplosis* live in simple galls and pupate in the ground. Adults of those two genera are generally similar, but larvae of *Caryomyia* have many derived character states compared to larvae of *Caryadiplosis* that have conserved their primitive form (Gagné 2008).

The described species of *Celticecis* fall into five distinct groups. We expect that the molecular analysis (Scheffer *et al.*, in preparation) will confirm these general categories and elucidate further relationships.

Celticecis japonica stands alone for its short ovipositor and the presence of four lateral papillae on each side of the spatula. These character states are the most primitive for the genus. This species is geographically separated from the other known species by the Pacific Ocean.

Nine species of the 21 North American species, viz., *C. aciculata*, *C. acuminata*, *C. capsularis*, *C. conica*, *C. cupiformis*, *C. pilosa*, *C. spiniformis*, *C. subulata*, and *C. supina*, appear to compose a natural group. All form galls on the leaf lamina except for *C. supina* whose galls are attached to veins, usually minor ones. These species share a striking synapomorphy of the second instar on which the lateroventral spinules of the thorax are appreciably larger than elsewhere. They also share the loss of one pleural and one sternal papilla on each side of the first through seventh larval abdominal segments and of one ventral papilla on the eighth abdominal segment. In addition, females share a moderately long ovipositor, but with the quadrate eighth tergite not longitudinally divided and the fused cerci only ca. twice as long as high.

Another group comprises four species with galls also on the leaves but either along major veins or in the forks of veins. These are *C. globosa*, *C. pubescens*, *C. pyriformis*, and *C. wellsi*. These species, except for *C. pyriformis* whose female is yet unknown, share a moderately long ovipositor with the quadrate eighth tergite not longitudinally divided and short, fused female cerci that are no longer than high. These four species also share certain losses in larval papillae, q.v., under *C. pubescens*.

There are no apparent similar species to *Celticecis cornuata.* Unlike all other species of the genus the second instar has no trace of a spatula and the third instar spatula appears closest to a primitive type for the genus. Adults of this species are unfortunately still unknown. Galls appear along leaf veins but, unlike other leaf-galling species, develop a basal callus that persists on the leaf.

The last group comprises the stem-galling species. Galls of each of them can occasionally be found also on leaves but, when they are, the leaves become more or less deformed. These are *C. celtiphyllia*, *C. connata*, *C. expulsa*, *C. ovata*, *C. oviformis*, *C. ramicola*, and *C. semenrumicis*. The six species with known females (that of *C. ovata* is unknown) share an elongate female eighth tergite that is more or less divided longitudinally and a long cercus that is about three times as long as high. Unlike the remaining American species, the larvae have retained most of the basic complement of papillae. They also have the largest body size in the genus.

Biology

Celticecis species have one generation per year. Adults emerge in early spring and the females lay their eggs on very young elongating stems and leaves. Galls are complex and most have one larval chamber with a single larva in each (Fig. 1). The galls of *C. connata* are exceptional in that they are most often aggregate galls with two or more larval chambers (Fig. 14). Galls of most species develop quickly, already containing young second instars by the time leaves are fully unfurled. The galls mostly grow to their full length before broadening to their ultimate size. Young galls of two or more species may look alike during early development and often occur on the same leaf (Fig. 2). Galls are fully developed before the larvae turn into the ultimate third instar. When full-grown, larvae spin webbing around the inside of the larval chamber, most prominently apically as a circular cap at some distance below the apex (Fig. 40). Larvae eventually permanently reverse their position in the chamber so that their anterior end faces the gall apex. In due course galls dehisce and the larvae diapause through the winter. Pupae develop in later winter or early spring. They then force their way out of the cocoon and halfway through the gall apex, whereupon the adult breaks through the pupal thoracic cuticle. Larvae of at least some species, viz. *C. connata*, *C. expulsa*, and *C. pubescens*, may remain in the galls as larvae through at least another year and pupate only the following spring.

The position of the gall on the plant for each species is presumably determined by the oviposition site, but hatchlings may also play a part if they are able to crawl. Seven species form galls on the present year's stems or petioles and only rarely on leaf bases. The remaining species are found only on the leaves. Some of these leaf-galling species are always found on the lamina, others always connected to veins, and two species always at vein forks. The underside of the leaf is the preferred site, but galls of all leaf-galling species can occasionally be found also on the upper side.

All *Celticecis* second instars except *C. cornuata* have a spatula. The second instar spatula is found in some or all species of several gall-forming genera (see Gagné 2008: 11) but this development is evidently separately derived in the genera where it appears. The second instar spatula, as well as that of the third instar in at least *Celticecis*, is presumably used as a scraper to encourage growth of food-producing cells in the galls.

Most stem galls tend to dehisce in spring, but those on the leaves may remain long after the third instars have formed cocoons, even until leaf fall in autumn. While galls and larvae of most species develop very early in spring, a few develop later in the season even though their eggs were evidently deposited in spring. *Celticecis globosa* is the latest to appear in the season, with galls still not fully developed as late as September.

Adults of eight species of *Gastrancistrus* (Hymenoptera: Pteromalidae) and seven of *Trichacis* (Hymenoptera: Platygastridae) were regularly reared in spring from galls of *Celticecis*. A *Gastrancistrus* was reared from almost every species of *Celticecis*, but most of the specimens remain unidentifiable and probably represent species new to science (M. Gates, pers. comm.). The *Trichacis* spp. were reared from several galls of *Celticecis* and almost all identified either to or near a particular species (T. Nuhn, *in litt.*). These definite host records are the first known for these *Trichacis* species. Other Hymenoptera reared from *Celticecis* galls but less commonly were: *Tenuipetiolus* sp. (Eurytomidae), *Torymus* spp. (Torymidae), *Platygaster* sp. (Platygastridae) and *Brasema* sp. (Eupelmidae). These parasitoids are listed under the individual *Celticecis* species from which they were reared. It is interesting that some parasitoids emerged from galls in company with their *Celticecis* hosts in the second calendar year following collection of the galls.

Distribution

Celticecis is presently known only from the Holarctic Region, with 21 species from North America (the present study), the Japanese *C. japonica* and an undescribed species from Turkey (Gagné & Moser 1997). The Turkish species, known only from galls and second instar larvae, cannot be characterized properly for description from the few specimens available. Descriptions of two other species from Japan are in preparation by S. Sato and J. Yukawa (pers. comm.) and not considered further in this paper.

In North America, *Celticecis* spp. are restricted geographically rather than by host. This is a similar situation to the gall midges on hickories which do not distinguish among species within a section of their host genus (Gagné 2008). As an ex-

ample, *C. subulata* (Map 19) is known from sugarberry, dwarf hackberry and netleaf hackberry, but is restricted to the southern U.S. much below the southern extent of sugarberry. Nonetheless, the geographic pattern of various species is not always so clear-cut. For instance, *Celticecis spiniformis* (Map 18) occurs on the same three hosts as *C. subulata* and, additionally, northern hackberry. It is the most widespread and most commonly found species throughout the season in most of the eastern half of the U.S. and is the only *Celticecis* species so far known from New York and New England, yet has not been found in Florida. The reason for its absence there is unknown and does not appear to be due to lack of collecting. K.L. Hibbard collected hackberry galls for us in a number of eastern and central Florida localites over a period of three years; J. Brambila collected several times during one season in the vicinity of Gainesville; and one of us (RJG) made a special trip to eastern and central Florida to collect on hackberries, but none of us ever collected this species there. *Celticecis spiniformis* was recorded from Alachua Co., Florida in Hodges *et al.* (2006) but with no illustration. This record could refer instead to a gall of one of the two look-alikes, *C. aciculata* or *C. subulata* (Fig. 2).

As with *Caryomyia* (Gagné 2008), *Celticecis* is rare where populations of the host are isolated. For example, while sugarberry can be found at many sites along the Lower Rio Grande Valley in southern Texas, that population is discontinuous from the closest part of its main range, which begins south of San Antonio and continues northwards (Little 1971). Collecting in several places in the lower Rio Grande Valley in 2010, RJG found galls of only one species, *C. connata*, and only at one site, in Mission, Texas. In Arizona, where only reticulate hackberry grows and then discontinuously, three species, *C. aciculata*, *C. connata*, and *C. pubescens*, were found at each of two sites by our colleague, R. Fitzgibbon. One of the species was collected only once, the others repeatedly.

Species Treatments

Celticecis aciculata Gagné, new species

Description.—*Gall* (Figs. 1–2). On underside of leaf, rarely above, between veins, often in groups; usually cylindrical, sometimes widened at base, basal margin rounded or sharply angled, tip always abruptly narrowed a short distance before apex; glabrous, usually naked, rarely with sparse, short, stiff hairs, green, turning tan to brown; 3.2–4.0 mm high and 2.0–2.5 mm wide at base; connection to leaf circular, flat, ca. 1/3 width of gall base, apparent on opposite side of leaf as slight discoloration, rarely as a small convexity; gall in cross section thickest surrounding base of cylindrical larval chamber, thinning gradually towards apex.

Adult. Antenna with 13–14 flagellomeres in male (n=5) and 12–14 in female (n=5). Wing length: male, 1.6–2.1 mm (n=5); female, 1.5–2.1 mm (n=5). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with mostly single row of posterior setae intermixed with scales covering posterior 2/3 of sclerite; eighth tergite weakly sclerotized, with single row of sparse posterior setae and no scales. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite ca. ½ width of sixth tergite, quadrate, slightly wider than long, with 2–3 rows of posterior setae, scales covering posterior 2/3; eighth tergite quadrate, slightly longer than wide, undivided longitudinally, with mostly double row of short setae along posterior margin; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high. Ninth segment to end of fused cerci 0.34–0.41 mm long and 2.3–2.5 times as long as sixth tergite (n=5).

Pupa (Figs. 75–76). Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, apex in lateral view acutely triangular. Face without protuberances.

Larva. **Third instar**: Length, 1.6–2.2 mm (n=10). Body elongate-ovoid, weakly sulcate intersegmentally, anterior and posterior ends blunt except for pointed head. Spatula (Fig. 128): shaft rectangular, well pigmented anteriorly and centrally, usually in the shape of a semicircle, weakly pigmented laterally and posteriorly; anterior teeth narrow, acutely pointed and separated from one another by a distance greater than their length. Papillae: 4 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 4 terminals; 2 sternals on both thoracic and abdominal

segments; 2 laterals on each side of midline on thoracic segments, their setae if apparent shorter than socket diameter; 1 ventral per side on each segment of thoracic and first through eighth abdominal segments, that of eighth abdominal lacking the seta. Dorsal, pleural, and terminal setae shorter than spiracular width. **Second instar**: Length 0.8–1.3 mm (n=8). Spatula (Fig. 150): with acute anterior tooth ca. 1/2 as long and 1/3 as wide as broad shaft. Lateroventral spinules appreciably larger on thorax than on abdomen. Dorsal, pleural and terminal setae barely longer than width of adjacent spiracles, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type material.—*Holotype*: third instar larva, on sugarberry, Alexandria, Louisiana, IX-21-2008, J.C. Moser, deposited in USNM.

Etymology.—The name *aciculata* refers to the abruptly narrowed and pointed gall apex.

Affinities.—See under *C. spiniformis*.

Biological notes.—Occasionally, galls are splayed outwards basally as for galls of *C. spiniformis*, but *C. aciculata* galls are always abruptly narrowed apically rather than tapered. In Alexandria, Louisiana, galls can be found in early May when they already contain clear or white second instars. By mid-June many larvae have reached the third instar. By early July some have spun cocoons and have turned from white to light yellow, at least anteriorly. The cocoons abut the base of the nipple at the end of the gall. By the end of August galls begin to dehisce but many with viable larvae remain on the leaves until leaf drop in autumn. *Gastrancistrus* sp. from Alexandria, Louisiana and *Torymus* sp. from Sycamore Canyon Wilderness, Arizona were reared in spring from galls of *C. aciculata* collected the previous summer.

Distribution (Map 1).—A southern U.S. species found from Georgia and Florida and west to Arizona, *C. aciculata* was found on sugarberry, dwarf hackberry and netleaf hackberry. **Arizona**, netleaf hackberry: Camp Verde; Sycamore Canyon Wilderness. **Arkansas**, sugarberry: 4.4 mi. NW Emmet. **Florida**, sugarberry: Basinger, Edgewater, Fort Pierce, Gainesville, Georgiana, Glencoe, Indiantown, Micanopy, Mims, Port Orange, Titusville. **Georgia,** sugarberry: Musella; dwarf hackberry: Houston Co. **Louisiana**, sugarberry: Alexandria, New Orleans, Pineville. **Mississippi**, sugarberry: Greenville, Grenada, Stoneville. **Texas**, sugarberry: Belton, Bertram, Burnet, College Station, Columbus, Donie, Georgetown, Lufkin, Marlin, Nacogdoches, Temple.

Specimens of *C. aciculata* examined.—All from sugarberry except Arizona record from netleaf hackberry. **Arizona**: Sycamore Canyon Wilderness, VII-11-2009, R. Fitzgibbon & B. Geils, 5 third instars, and 1 ♂, 2 ♀, emerged IV-8-2010. **Arkansas**: 4.4 mi NW Emmet, VIII-20-2009, T.O. Robbins, 1 third instar. **Florida**: Yates Marsh, Basinger, VI-3-2009, K. Hibbard, 2 second and 3 third instars; Edgewater, VI-26-2009, K. Hibbard, 2 third instars; Indiantown, V-9-2009, 2 second and 4 third instars; Mims, V-27-2010, K. Hibbard, 2 ♂, 2 ♀, 2 pupae, emerged III-10-2011; Titusville, VI-26-2009, K. Hibbard, 5 third instars. **Louisiana**: Alexandria, IX-21-2008, JCM, 2 third instars; VI-21-2009, JCM, 1 third instar; VIII-7-2009, JCM, 5 third instars, and 1 ♂, 2 ♀, emerged III-17 to IV-1-2010; VII-5-2010, JCM, 5 ♂, 6 ♀, 5 pupal exuviae, emerged III-24 to IV-4-2011. **Mississippi**: Greenville, IX-4-2008, RJG, 2 third instars; Grenada, IX-3-2008, RJG, 2 third instars; Stoneville, IX-5-2008, RJG, 2 third instars, and 2 ♂, 5 ♀, 3 pupal exuviae, emerged IV-22-2009. **Texas**: College Station, VIII-3-2009, RJG, 2 third instars; Georgetown, VIII-5-2009, RJG, 1 third instar; Kurth Lake, near Lufkin, X-22-2009, JCM, 3 third instars.

Celticecis acuminata Gagné, new species

Description.—*Gall* (Figs. 3–4). On lamina on underside of leaf, often in groups; upright, bulbous at base, tapering beyond mid-length to gall apex; green, turning tan or gray, covered with moderately long white hair, hair not obscuring granulose gall surface; ca. 4.0 mm long by 2.5 mm at widest; apparent on opposite side of leaf as an inconspicuous convexity; gall in cross section with elongate-ovoid larval chamber with thick, woody walls widest near mid-length.

Adult. Antenna with 15 flagellomeres in male (n=1) and 15 in female (n=4). Wing length: male, 2.0 mm (n=1); female, 1.9–2.3 mm (n=4). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with 2–3 rows of posterior setae intermixed with scales covering posterior 2/3 of sclerite; eighth tergite weakly sclerotized, with single row of sparse posterior setae and no scales. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites

with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite ca. ½ width of sixth tergite, quadrate, slightly wider than long, with mostly single row of posterior setae, scales covering posterior half; eighth tergite quadrate, slightly longer than wide, undivided longitudinally, with mostly two rows of short setae along posterior margin; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high. Ninth segment to end of fused cerci 0.41 mm long and 2.4–2.5 times as long as length of sixth tergite (n=3).

Pupa (Figs. 77–78). Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, acutely triangular in lateral view. Face without protuberances.

Larva. **Third instar**: Length, 1.8–2.9 mm (n=8). Spatula (Fig. 129): shaft trapezoidal to triangular, the acute anterior teeth ca. 1/4 as long as shaft, joined at their bases, either closely approximated or well separated. Papillae: 4 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side on thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 4 terminals; 2 sternals on thoracic and abdominal segments; 2 laterals each side of midline, their setae usually prominent, sometimes only as long as socket diameter; 1 ventral per side on each segment, all with seta except on eighth abdominal segment. Dorsal, pleural, and terminal setae as long as spiracular width, the ventral setae slightly shorter. **Second instar:** Length 1.1–1.9 mm (n=7). Spatula (Fig. 151): with acute anterior tooth ca. ½ as long and 1/3 as wide as broad shaft. Lateroventral spinules appreciably larger on thorax than on abdomen. Dorsal, pleural, and terminal setae longer than width of adjacent spiracles, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type material.—*Holotype*: third instar larva, on sugarberry, Kittawa, Kentucky, IX-1-2008, RJG, deposited in USNM.

Etymology.—The name *acuminata* refers to the gall's tapering to a point from its bulbous base.

Affinities.—See discussion under *C. spiniformis*.

Biological notes.—Young galls were found in Alexandria, Louisiana on only partially expanded leaves. Galls could be found on leaves into September. The cocoon extends to the base of the tapered portion of the gall that breaks off upon eclosion of the adults.

Distribution (Map 2).—This is an uncommon species found in southeastern and midwestern U.S. on northern hackberry, dwarf hackberry and sugarberry. It is one of the few species apparently absent from Louisiana and Texas. **Arkansas**, sugarberry: 4.4 mi NW Emmet. **Florida**, sugarberry: Edgewater. **Georgia**, dwarf hackberry: Lake Tobesofkee, Bibb Co. **Kentucky**, northern hackberry: Kuttawa. **Iowa**, northern hackberry: Ames. **Louisiana**, sugarberry: Alexandria. **Mississippi**, sugarberry: Grenada. **Ohio**, northern hackberry: Batavia, Sandusky. **Virginia**, northern hackberry: Suffolk.

Specimens of *C. acuminata* examined.—**Arkansas**, sugarberry: County Rd 53, 4.4 mi NW Emmet, VIII-20-2009, T.O. Robbins, 3 third instars. **Florida**, sugarberry: Edgewater, VI-26-2009, K. Hibbard, 3 second and 3 third instars. **Georgia**, dwarf hackberry: Lake Tobesofkee, Bibb Co., VI-5-2011, J. & R. Payne, 5 third instars. **Kentucky**, northern hackberry: Kuttawa, IX-1-1908, RJG, 2 third instars. **Iowa**, northern hackberry: Ames, IX-27-2010, M.J. Hatfield, 2 third instars. **Louisiana**, sugarberry: Alexandria, VI-21-2009, JCM, 2 second instars. **Mississippi**, sugarberry: Grenada, IX-2-2008, RJG, 3 third instars, and 2 ♂, 5 ♀, 1 pupa, 3 pupal exuviae, emerged V-26 to V-28-2009. **Virginia**, northern hackberry: Suffolk, VI-16-2010, RJG, 4 second instars.

Celticecis capsularis (Patton)

capsularis Patton 1897: 248 (*Cecidomyiaceltis*), with reference to gall #33 of Riley 1890: 613; Felt 1918: 123 (*Cecidomyia*); Felt 1940: 232 (*Cecidomyia*); Gagné 1983: 437 (*Celticecis*).

painteri Felt 1935: 7 (*Phytophaga*); Painter 1935: 87, Plate 1, Fig. 6 (gall) (*Phytophaga*); Felt 1940: 234, Plate 40, Fig. 7 (*Phytophaga*); Gagné 1983: 437 (*Celticecis*). **New synonym**.

Description.—*Gall* (Figs. 5–6). On leaf lamina on underside of leaf; depressed, circular, the sides conspicuously sulcate with 10 or more furrows, broadest at mid-length, apex with central spine; green, turning brown, granular, moderately long-haired but hairs not obscuring surface; ca. 2 mm high and 3–4 mm broad; connection to leaf conical, fitting into slight depression of leaf, a slight brown convexity apparent on reverse side of leaf; wall thick laterally, thin apically; larval chamber ovoid, extending the length of gall, lined with brittle tissue distinct from remainder of gall.

Adult. Antenna with 14–16 flagellomeres in male (n=5) and 14–15 in female (n=5). Wing length: male, 2.4–2.6 mm (n=5); female, 2.3–2.6 mm (n=5). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with double row of posterior setae and no scales; eighth tergite sclerotized on anteriorly, without posterior setae or scales. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite 1/2 the width of sixth tergite, quadrate, slightly wider than long, with 2 rows of posterior setae, and few scales posteriorly; eighth tergite quadrate, slightly longer than wide, undivided longitudinally, with mostly double row of short setae along posterior margin; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high. Ninth segment to end of fused cerci 0.38–0.45 mm long and 2.9–3.2 times as long as length of sixth tergite (n=5).

Pupa (Figs. 79–80). Antennal bases foreshortened, bilaterally compressed, keel-like ventrally, closely adjacent, acutely triangular in lateral view. Face with convex protuberance on each side.

Larva. **Third instar:** Length, 1.9–2.4 mm (n=10). Body ovoid, barely sulcate intersegmentally, the anterior and posterior ends blunt except for the pointed head. Spatula (Fig. 130): vestigial, a small obtusely triangular or lunulate pigmented area between the lateral setae. Papillae: 4 dorsals, except 2 on eighth abdominal segment; 1 pleural on each side of thoracic and first through eighth abdominal segments; 4 terminals; 2 sternals on both thoracic and first through seventh abdominal segments; 2 laterals per side, setae if apparent shorter than socket diameter; 1 ventral per side on each thoracic and first through eighth abdominal segments, that of eighth abdominal segment lacking the seta. All papillar setae except for laterals shorter than spiracle width. **Second instar**: Length, 0.9–1.4 mm (n=6). Spatula (Fig. 152): cuneiform, widest at base, tapering to acute apical tooth, the shaft not as darkly pigmented as tooth. Lateroventral spinules slightly larger, not always appreciably so, on thorax than on abdomen. Dorsal and pleural setae no longer than width of adjacent spiracles, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type material.—*Cecidomyiaceltis capsularis* Patton: *Syntypes*: 23 galls on three separate pinned leaves, one including also a gall of *C. acuminata*, not considered a syntype because the specimen was not characterized in Riley's (1890) description, the basis of Patton's description. Each pin is labeled: "*Cecidomyia* on *Celtis texana* [= *Celtis laevigata*,] Columbus Tex[,] 7/17/79 [, C.V.] Riley."

Phytophaga painteri Felt: *Lectotype*: female, **here designated**, and 8 male paralectotypes, Austin, Texas, 10-III-23, R.H. Painter, #22, a3306, deposited in NYSM. The specimens are all on one slide and uncleared. Felt (1935) reported the hosts as *Celtis missisippiensis* (=*Celtis laevigata*) and *Celtis reticulata* and that the specimens were collected at Austin and San Antonio, Texas.

Etymology.—Patton (1897) named this species *capsularis* based on Riley's (1890) remark that the rosette-shaped galls resembled the seed capsule of hibiscus. With the name *painteri*, Felt honored Reginald H. Painter, who collected the species and was a professor at what is presently Kansas State University in Manhattan, Kansas.

Affinities.—See discussion under *C. spiniformis*.

Biological notes.—The gall grows lengthwise first, then laterally, developing the separate lobes as it expands. Full grown larvae are yellow and fill the entire cavity. In Alexandria, Louisiana galls with second instars were found in late March on newly expanded leaves and also later in the season. In Fort Pierce, Florida, fully-formed galls were found in early April. By mid-May some galls have fully-developed larvae. Galls with cocooned larvae may dehisce any time during the summer but many remain attached to the leaves through autumn. In spring pupae break through a circular opening that develops just below the apical spine.

Gastrancistrus sp. from Alexandria, Louisiana, and Temple, Texas, and *Torymus* sp. from Temple, Texas, were reared in spring from galls of *C. capsularis* collected the previous summer.

Distribution (Map 3).—This is a southeastern U.S. species taken on all hackberries within its range: **Arkansas**, sugarberry: 4.4 mi. NW Emmet. **Florida**, sugarberry: Basinger, Fort Pierce, Gainesville, Indiantown, Mims, Port Orange. **Georgia,** sugarberry: Musella and Monroe Co; dwarf hackberry: Houston Co. **Louisiana**, sugarberry: Alexandria, Pineville. **Mississippi**, sugarberry: Greenville, Grenada, Stoneville. **Tennessee**, northern hackberry: Nashville. **Texas**, sugarberry: Austin (also on netleaf hackberry), Belton (also on netleaf hackberry), College Station, Columbus, Donsie,

Holland, Lufkin, Luling, Marlin, Nacogdoches, San Antonio (Painter 1935), Sparks (Bell Co.), Temple.

Specimens of *C. capsularis* examined, all from sugarberry.—**Florida**: Yates Marsh, Basinger, VI-3-2009, K.L. Hibbard, 3 third instars; Paleo Hammock, Fort Pierce, IV-29-2009, K.L. Hibbard, 5 third instars; Indiantown, V-7-2009, K.L. Hibbard, 3 third instars; Indiantown, V-26-2010, K. L. Hibbard, 2 ♂, 3 ♀, 3 pupal exuviae, emerged II-12–14-2011. **Louisiana**: Alexandria, VI-20-2010, JCM, 5 ♂, 5 ♀, 3 pupae, emerged III-20-2011. **Mississippi**: Greenville, IX-4-2008, RJG, 2 third instars; Grenada, IX-20-2008, RJG, 1 third instar; Stoneville, IX-5-2008, RJG, 3 third instars, 1 ♀, emerged IV-30-2009. **Texas**: Austin, type series of *C. painteri*; Belton, VII-16-2009, T.O. Robbins, 3 third instars; Belton, VIII-4-2009, T.O. Robbins & RJG, 5 ♂, 6 ♀, emerged II-10–26-2011; College Station, VIII-3-2009, RJG, 3 third instars; Luling, J. R. Riemann, 1 ♂, emerged III-3-1957; Kurth Lake, near Lufkin, V-3-2009, JCM, 3 second and 3 third instars.

Celticecis celtiphyllia (Felt)

celtiphyllia Felt 1908: 371 (*Mayetiola*); Felt 1915b: 216 (*Phytophaga*); Wells 1916: 271, Plate XVII, Fig. 9a, Plate XVIII, Figs. 9, 9a–b (*Phytophaga*); Felt 1918: 122 (Fig. 118), 124 (*Phytophaga*); Felt 1940: 233 (Fig. 192), Plate 40, Fig. 5. (*C. connata*, not *celtiphyllia*) (*Phytophaga*); Gagné 1983: 437 (*Celticecis*; lectotype designation).

Description.—*Gall* (Figs. 7–10; Plate 1, Fig. 9c; Plate 2, Figs. 9, 9 a–b). On twigs, petioles or major veins on either leaf surface and often distorting the leaf, usually in crowded clusters; campanulate, the flattened apex with central, fluted, elongate projection; surface green, turning buff or brown, entirely covered with long hairs not obscuring surface, lower portion smoothly rounded, upper portion beyond widest dimension may be furrowed; ca. 6 mm long and 5 mm in diameter at greatest width, distal appendage a further 1–2 mm long; connection to plant not prominent, ca. 1/3 gall diameter; wall woody, thin near base, much thickened at mid-length and beyond, larval chamber pear-shaped, the larva living in larger basal portion.

Adult. Antenna with 20–21 flagellomeres in male (n=5), 21–25 in female (n=7). Wing length, male 2.9–3.6 mm (n=4); female, 2.6–3.6 (n=7). **Male abdomen**: First through third tergites with 1–2 rows of posterior setae, and fourth through seventh tergites with 2–3 rows of posterior setae, lateral setae present near mid-length on sixth and seventh tergites only, and all covered with scales; eighth tergite less pigmented posteromesally than elsewhere, with posterolateral setae and scattered scales. Terminalia (Figs. 58–60, 119–120): gonostylus tapering from broad base to apex, setulose only on basal third dorsally, on basal half ventrally, remaining surface ridged and naked except for scattered setae. **Female abdomen** (Figs. 66–68, 124): First through sixth tergites with mostly single row of posterior setae except fifth and sixth with 2 rows, without lateral setae, and covered with scales; seventh tergite ca. ½ width of sixth tergite, quadrate, slightly longer than wide, with 2–3 rows of posterior setae, scales covering almost entire sclerite; posterior pigmented extensions of seventh tergite continuous to eighth; eighth tergite formed of two well-separated, elongate sclerites ca. 1/3 longer than seventh tergite, with short, scattered, tiny setae posteriorly. Ovipositor elongate-protrusible; ninth segment to end of fused cerci 1.1–1.2 mm long and 3.7–3.9 times as long as sixth tergite; cerci elongate-cylindrical, ca. 3 times as long as high (n=5).

Pupa (Figs. 71–74). Antennal bases pyramidal, their apices diverging and well separated, barely acute in lateral view. Face with pair of low facial convexities at mid-length, not always prominent, sometimes absent.

Larva. **Third instar** (Figs. 95–98): Length, 3.0–4.3 mm (n=10). White to yellow-orange. Body widest at middle, tapering to ends, broader than thick, deeply sulcate between segments. Spatula (Fig. 132): with two narrow, acute anterior teeth each 2× as long as basal width and separated from one another by distance greater than basal width; large shaft widest anteriorly, concave anteriorly between the teeth and on lateral margins. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals per side on all thoracic and abdominal segments; 8 terminals; 2 sternals without setae on thoracic and first through seventh abdominal,segments; 2 laterals per side with barely apparent setae, shorter than papillar base if apparent; 1 setose ventral per side on thoracic and first through seventh abdominal segments and 4 on eighth abdominal these last only rarely with seta on one of the four papillae. Dorsal, pleural and terminal setae long, almost 2× as long as width of spiracles. **Second instar**: Length, 1.2–2.0 mm (n=10). White to yellow. Spatula (Fig. 153):

robust, with large, acute anterior tooth, 1/2 the width and more than 1/2 length of quadrate shaft. Spinules on venter of collar segment appreciably more numerous and closer together than elsewhere. Lateroventral spinules not larger on thorax than elsewhere. Length of papillae relative to spiracles as for third instar.

Type material.—*C. celtiphyllia: Lectotype*: designated by Gagné (1983: 437), male, Keokuk, Iowa, em. V-1900, J.M. Schaffer, C913, Pergande #9015, USNM. Paralectotypes, 1 male, 2 females, same data as lectotype, and 1 male, not *C. celtiphyllia* and not further identified, Corpus Christi, Texas, em. II-3-1897, E.A. Schwarz. The galls from which the Keokuk type series issued are preserved in the USNM.

Etymology.—The name *celtiphyllia* was presumably coined to mean "on leaf of *Celtis*."

Remarks.—Felt's (1908) original description from specimens sent him by Pergande at the USNM did not specify a particular gall as the source of this species, stating only that the series was "bred from *Celtis* leaves." Felt (1915b) described the male and female in more detail and reported the species from both Keokuk, Iowa, and Corpus Christi, Texas. Felt (1918) placed the name *oviformis* Patton in parentheses below *celtiphyllia* presumably to indicate synonymy, but the two species are distinct. Wells (1916) made fine histological drawings of the galls that are reproduced here (Pls. 1–2).

Affinities.—This is the only North American species that has lateral setae on the abdominal tergites, although only on the sixth and seventh segments and only on the male. The Japanese *C. japonica* has lateral setae on the third through seventh tergites of both sexes. Although both species have lateral setae on at least some tergites, the resemblance ends there because their ovipositors are as different as can be for the genus. That of *C. japonica* is primitively short and barely protrusible, that of *C. celtiphyllia*, in company with *C. expulsa*, having the longest for the genus. Among the North American species, *C. celtiphyllia* is unique, in addition to having lateral tergal setae in the male, for the widely spread pupal antennal apices and the field of numerous spicules on the venter of the second instar collar segment. This species shares the long cerci and elongate eighth tergite found in females of other stem-galling *Celticecis* species, viz., *C. connata*, *C. expulsa*, *C. oviformis*, *C. ramicola*, and *C. semenrumicis*. It is tempting to postulate some affinity among these species for these shared characters of the female, but long cerci and eighth tergites may be separately derived adaptations for laying eggs deep into buds of hackberries.

Biological notes.—For his gall description, Felt (1915b) cited Pergande's unpublished notes, as follows: "very hard, obconic, the upper extremity produced as a long, slender nipple; at the base five or six low ridges. The galls are smooth inside and divided by a delicate though dense web into two compartments, the larva occurring in the lower." This describes well the galls that are still at the USNM. The illustrations in Felt (1918, 1940) showed a separate series of young galls of this species growing on a stem, but their provenance was not indicated. With their slender shallot-like shape these galls look rather different from full-grown galls, but that is how the galls appear when the larvae are early second instars and before the galls broaden considerably. In Fort Pierce, Florida, galls were full grown with active second instars by March 7. Larvae had formed cocoons and were dehiscing by May 9. In both Louisiana and West Virginia, third instars were present by June 30. Galls did not always dehisce readily and were occasionally found with healthy larvae as late as September in West Virginia. Both second and third instars are very active and may be white to yellow-orange.

Gastrancistrus sp. was reared in spring from galls of *C. celtiphyllia* collected the previous summer in West Virginia.

Distribution (Map 4).—This species is widespread in eastern U.S. on northern hackberry, dwarf hackberry and sugarberry. Galls of *C. celtiphyllia* are known from: **Arkansas**, sugarberry: 4.4 mi NW Emmet. **Florida**, sugarberry: Edgewater, Indiantown, Mims, Fort Pierce. **Georgia**, dwarf hackberry: Rum Creek Wildlife Management Area, Monroe Co. **Iowa**: northern hackberry, Keokuk. **Kansas**, northern hackberry: Lawrence. **Louisiana**, sugarberry: Alexandria, Pineville. **Maryland**: northern hackberry, Williamsport. **Mississippi**, sugarberry: Grenada. **Ohio**, northern hackberry: Sandusky (Sears 1914, fig. 34). **Texas,** sugarberry: Belton, Bertram, Burnet, Donie (also on netleaf hackberry), Georgetown, Temple. **West Virginia**, northern hackberry: Falling Waters.

Specimens of C. *celtiphyllia* examined.—**Florida**, sugarberry: Indiantown, V-9-2009, K.L. Hibbard, 2 second and 4 third instars; Paleo Hammock, Ft. Pierce, IV-29-2009, K.L. Hibbard, 1 second instar. **Georgia**, dwarf hackberry: Rum

Creek Wildlife Management Area, Monroe Co., VI-6-2011, J. & R. Payne, 2 third instars. **Iowa**: Keokuk, lectotype and paralectotypes of *C. celtiphyllia* plus 3 pupal exuviae associated with that series. **Louisiana**, sugarberry: Alexandria, V-23-2010, J.C. Moser, 2 second instars; Pineville, IV-25-2009, J. Moser, 3 second instars. **Maryland**: northern hackberry: Williamsport, VII-11-2010, RJG, 3 third instars. **Texas**, sugarberry except Donie on netleaf hackberry: Austin, emerged III-29-1932, R.H. Painter, 1 ♂, 1 ♀; Donie, VIII-21-2009, T.O. Robbins, 2 third instars; Temple, VII-15-2009, T.O. Robbins, 3 third instars, 12 ♀, 5 pupae, emerged IV-13 to V-5-2010; Temple, 3-5 mi S midtown, VIII-4-2009, T.O. Robbins & RJG, 2 second instars. **West Virginia**, all from northern hackberry at Falling Waters, collected by RJG: VIII-16-2008, 2 third instars, 10 ♂, 10 ♀, 5 pupae, emerged IV-17 to V-26-2009; VI-14-2009, 4 second instars; VII-21-2009, 3 ♂, pupa, emerged IV-7-2010; and VI-8-2010, 4 second instars.

Celticecis conica Gagné, new species

Description.—*Gall* (Figs. 11–12). On leaf lamina on underside of leaf, found singly or in groups; upright, short-conical, evenly tapered from circular unsplayed base to narrowly rounded apex; naked, glabrous, green, turning yellow to brown; ca. 2.5 mm high and 1.5 mm wide at base; connection to leaf circular, flat, ca. 1/3 width of gall base; apparent on opposite side of leaf as slight, sometimes discolored convexity; gall in cross section thick around base and thinning gradually toward apex, the subcylindrical larval chamber as long as gall.

Adult. Antenna with 12–13 flagellomeres in male (n=5) and 11–12 in female (n=3). Wing length: male, 1.5–1.7 mm (n=5); female, 1.5–1.7 mm (n=5). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with single row of posterior setae intermixed with scales, remainder of sclerite without scales; eighth tergite weakly sclerotized, with 0–2 setae posteriorly. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen** (Fig. 127). First through sixth tergites with single row of posterior setae, without lateral setae, and covered with scales; seventh tergite ca. 1/2 width of sixth tergite, quadrate, slightly wider than long, with single row of posterior setae, scales covering posterior half of sclerite; eighth tergite quadrate, slightly longer but narrower than eighth, undivided longitudinally, with several short setae along posterior margin; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high. Ninth segment to end of fused cerci 0.39 to 0.40 mm long and 3.3-3.5 times as long as length of sixth tergite (n=4).

Pupa (Figs. 81–82). Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, acutely triangular in lateral view. Face without protuberances.

Larva. **Third instar**: Length 1.4–1.7 mm (n=5). Body spindle-form, slightly sulcate intersegmentally, the anterior and posterior ends blunt except for pointed head. Spatula (Fig. 134): shaft roughly quadrate, weakly pigmented, especially anteromedially between the two anterior, acute, fairly closely approximated teeth. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 4 terminals; 2 sternals on both thoracic and abdominal segments; 2 laterals per side of midline with setae longer than socket diameter; 1 ventral per side on each segment of thoracic and first through eighth abdominal segments, that of eighth abdominal segment lacking a seta. All setae except those of laterals ½ to approximately as long as spiracular width. **Second instar**: Length 0.8–1.0 mm (n=3). Spatula (Fig. 154): generally triangular , tooth acute, shaft narrow anteriorly, widest posteriorly. Lateroventral spinules appreciably larger on thorax than on abdomen. Dorsal and pleural setae subequal to spiracular width, dorsals and pleurals of eighth abdominal segment appreciably shorter than terminals.

Type material.—*Holotype*: third instar larva, from gall on northern hackberry, Cabin John, Maryland, VIII-16-2010, RJG, deposited in USNM.

Etymology.—The name *conica* refers to the conical gall of this species.

Affinities.—The gall of this species is the smallest gall on hackberries after that of *C. cupiformis*, but is evenly conical rather than barrel-shaped. Females of both species have flagellomeres that are reduced in size and vestiture. See under *C. spiniformis* for further discussion.

Biological notes.—In Maryland, galls were first noticed on May 12, already with second instars. Full grown larvae were found in late June and had formed cocoons by early July. Some galls persisted on the leaf at least through mid-Septem-

ber. Third instars are white until full-grown when the anterior half of the body turns yellow.

Gastrancistrus sp. was reared in spring from galls of *C. conica* collected the previous summer at Cabin John, Maryland.

Distribution (Map 5).—This species is widely distributed in the eastern half of U.S. and occurs on both northern hackberry and sugarberry. Its relative rarity may be due to its small size, causing it to be overlooked; still, the fact that it was never found in Texas but occurs in Louisiana and Arkansas is remarkable. Galls are known from: **Arkansas**, sugarberry: 4.4 mi. NW Emmet. **Georgia**, sugarberrry: Augusta. **Kentucky**, northern hackberry: Georgetown, Winchester. **Louisiana**, sugarberry: Alexandria. **Maryland**, northern hackberry: Cabin John, Hancock, Potomac, Williamsport. **Ohio**, northern hackberry: Columbus, Union. **West Virginia**, northern hackberry: Cherry Run, Falling Waters, 6 mi. NW Hedgesville.

Specimens of *C. conica* examined.—**Arkansas**, sugarberry: 4.4 mi. NW Emmet, VIII-20-2009, T.O. Robbins, 2 third instars. K**entucky**, northern hackberry: Winchester, VI-23-2010, RJG, 3 second instars. **Maryland**, northern hackberry: Cabin John, VIII-7-2008, RJG, 1 third instar; Cabin John, VIII-16-2009, RJG, 2 third instars and 4 ♂, 6 ♀, 2 pupae emerged III-19 to 30-2010; Cabin John, VII-22-2010, RJG, 2 third instars and 2 ♂, 1 ♀, pupa, emerged IV-1/16-2011; Hancock, VII-5-2009, RJG, 2 third instars. **Ohio**, northern hackberry: Union, VI-22-2010, RJG, 2 third instars. **West Virginia**, northern hackberry: Falling Waters, VIII-16-2008, RJG, 1 third instar and 1 ♂ emerged IV-25-2009.

Celticecis connata Gagné, new species

Description.—*Gall* (Figs. 13–15). Usually along twig, occasionally on fruit, petiole or major veins of upper side of leaf; spheroidal, often irregularly so, woody, often consisting of two or more coalesced galls, usually with short nipple at apex; hairless, surface shining, becoming matte, red or green, turning brown; 5–7 mm high, 5–12 mm wide; connection to host small in extent, not apparent; walls thick, woody, but thin below nipple, the larval chamber ovoid.

Adult. Antenna (Fig. 55) with 17–19 flagellomeres in male (n=10) and 19–22 in female (n=10). Wing length: male, 2.5–3.1 mm (n=10); female, 2.8–3.5 mm (n=10). **Male abdomen**: First through sixth tergites with mostly double row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with 2–3 rows of posterior setae intermixed with scales that cover posterior 2/3 of sclerite; eighth tergite with double row of short setae posteriorly. Terminalia as for *C. celtiphyllia* except gonostylus (Fig. 61) thickest beyond mid-length, completely setulose. **Female abdomen** (Fig. 125): First through sixth tergites rectangular, ca. 2× as wide as long, with 3 rows of posterior setae laterally narrowing to one medially and evenly covered with scales; seventh tergite ca. 1/2 width of sixth tergite, quadrate, slightly wider than long, moderately concave laterally, with 4–5 rows of posterior setae, scales absent; eighth tergite 1/3 longer than seventh tergite, variably but only partly divided longitudinally, with scattered tiny setae at posterior end of each sclerite; ovipositor elongate-protrusible; cerci cylindrical, ca. 3 times as long as high. Ninth segment to end of fused cerci 0.90–0.95 mm long and 3.0–3.2 times as long as length of sixth tergite (n=5).

Pupa (Figs. 83–84). Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, diverging only apically, acutely triangular in lateral view. Face with a pair of convex protuberances.

Larva. **Third instar**: Length 2.4–5.5 mm (n=10). Yellow. Body shape spindle-form, as deep as broad at mid-length, sulcate intersegmentally. Spatula (Fig. 135) with quadrate shaft and two nearly equilateral anterior teeth separated from one another by their basal width or less. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals per side on all thoracic and abdominal segments; 8 terminals; 2 sternals on thoracic and 4 on abdominal segments; laterals 2–3 per side with barely apparent setae; ventrals 1 per side on each segment, with seta, except 2 per side on eighth abdominal segment, both with setae. Dorsal, pleural, terminal, and ventral setae 1/3–1/2 longer than spiracular width. **Second instar**: White. Length 1.5–2.2 mm (n=10). Spatula (Fig. 157): robust, more or less triangular, widest at base and ending in the broad, nearly equilateral anterior tooth. Spinules covering integument dense and uniform throughout. Length of papillae with same proportions as for third instar.

Type material.—*Holotype*: female, from galls collected VIII-5-2009 on sugarberry, Temple, Texas, T.O. Robbins and RJG, emerged III-18-2011, deposited in USNM.

Etymology.—The name *connata* means joined or growing together, with reference to the common habit of this species to form aggregate galls.

Affinities.—In a genus with fairly uniform male genitalia, *C. connata* and *C. expulsa* stand out for the shape of their gonostyli that are largest beyond mid-length. Unfortunately we have no males of *C. oviformis*, but the female and larvae of that species are generally similar to those of *C. connata* and *C. expulsa*.

Biological notes.—This is the only species of *Celticecis* to regularly form aggregate galls. In Alexandria, Louisiana, galls were found in late March before the leaves had hardened. By mid-April some galls contained small third instars, and by mid-May some larvae had formed cocoons. Galls begin to dehisce by mid-May, yet some remain on the twigs through November. Adults emerged from galls collected from Alexandria, Louisiana, and from Florida the spring following their collection, but emerged from galls collected from Pineville, Louisiana, and Bertram and Temple, Texas, only the second spring following their collection.

Several parasitoids were reared in spring from galls of *C. connata*: *Gastrancistrus* sp. from Fort Pierce and Indiantown, Florida; Alexandria and Pineville, Louisiana; and Bertram and Temple, Texas. *Torymus* sp. near *tubicola* (Osten Sacken) from Indiantown, Florida. *Brasema* sp. from Alexandria, Louisiana. *Tricacis* sp. near *celticola* Masner from Alexandria, Louisiana and Bertram, Texas. *Trichacis* sp. near *cornicola* (Ashmead) and *Trichacis* sp. from Bertram Texas. The parasitoids from Pineville, Louisiana, and Bertram and Temple, Texas emerged only the second season after the galls were collected.

Distribution (Map 6).—This is a mainly southern U.S. species found on all available hackberries. **Arizona**, netleaf hackberry: Sycamore Canyon Wilderness. **Florida**, sugarberry: Basinger, Fort Pierce, Indiantown. **Georgia,** sugarberry: Musella; dwarf hackberry: Houston Co. **Kansas**, northern hackberry: "western Kansas". **Kentucky**, northern hackberry: Bowling Green. **Louisiana**, sugarberry: Alexandria, Pineville. **Missouri**, northern hackberry: Columbia. **Texas**, sugarberry: Belton (also on netleaf hackberry), Bertram, Burnet, College Station, Donie, Georgetown, Holland, Mission, San Antonio (also on Lindheimer hackberry), Temple. **Virginia**, northern hackberry: Nassawadox.

Specimens of *C. connata* examined.—**Arizona**, netleaf hackberry: Sycamore Canyon Wilderness, VII-11-2009, R. Fitzgibbon & B. Geils, 2 third instars and 2 ♀, emerged IV-10-2010. **Florida**, sugarberry: Yates Marsh, Basinger, V-23-2010, K.L. Hibbard, 3 third instars; Fort Pierce, Paleo Hammock, IV-20-2010, K.L. Hibbard, 5 ♀, emerged III-2011; Indiantown, V-26-2010, K.L. Hibbard, 4 ♂, 5 ♀, emerged III- 3–24-2011. **Georgia**, sugarberry: Musella, V-3-2011, J. & R. Payne, 4 second instars. **Kansas**, northern hackberry: "western Kansas", summer 1944, R.H. Beamer, 2 third instars. **Kentucky**, northern hackberry: Bowling Green, V-27-2011, C. Eisemann, 2 third instars. **Louisiana**, sugarberry: Alexandria, III-29-2009, JCM, 6 second instars; Alexandria, IV-19-2009, JCM, 5 third instars; Alexandria, IV-25-2010, JCM, 5 third instars; Alexandria, VI-15–27-2010, JCM, 4 ♂, 8 ♀, emerged III-8–22-2011; Pineville, V-24-2009, JCM, 3 ♂, 5 ♀, emerged III-2011. **Missouri**, northern hackberry: Columbia, VI-24-1874, C.V. Riley, 1 third instar from paralectotype gall of *Cecidomyiaceltis oviformis*. **Texas**, sugarberry: Bertram, VIII-5-2009, RJG, 5 ♂, 5 ♀, emerged III-2011; Belton, VIII-4-2009, T.O. Robbins and RJG, 2 third instars; Burnet, VIII-5-2009, RJG, 3 third instars; Mission, XI-16-2010, RJG, 3 third instars; Temple, VIII-4-2009, T.O. Robbins & RJG, 2 third instars, and 5 ♂, 7 ♀, emerged III-3-2011.

Celticecis cornuata Gagné, new species

Description.—*Gall* (Figs. 16–17). On major vein, usually on lower surface of leaf; upright, elongate-cylindrical, unevenly tapered beyond 2/3 length to rounded, weakly recurved apex; basal margin irregularly angled; surface glabrous, naked, slightly furrowed, visible longitudinal veins slightly spiraling; green, usually turning red; 6–7 mm in length and up to 2 mm wide; connection to vein a prominent, circular, flat, persistent brown callus at least as wide as gall base; gall apparent on opposite side of leaf as slight thickening of vein; wall thin throughout, larval chamber of same shape as gall.

Adult, pupa. Unknown.

Larva. **Third instar**: Length 1.8–2.4 mm (n=2). Elongate-ovoid. Spatula (Fig. 136): anterior teeth acute, separated from one another by the length of their basal width; shaft somewhat longer than broad, more or less triangular, narrowest pos-

teriorly. Papillae: 4 dorsals on thorax, 6 on first through seventh abdominal segments and 2 on eighth abdominal; 2 pleurals on each side of thoracic and abdominal segments; terminals 4; sternals 2 on thoracic and first through seventh abdominal segments, all with setae; 2 laterals on each side of midline of thoracic segments, with conspicuous setae; 2 ventrals on thoracic and first through eighth abdominal segments, all setose; dorsal, pleural, and terminal setae shorter than spiracular width, the laterals not as long as other setae. **Second instar**: Length, 1.2–1.4 mm (n=3). Lateroventral spinules not appreciably larger on thorax than on abdomen. Spatula not present (Fig. 158). Setae not prominent on sternal papillae, sometimes not present on one of the pair on a segment; setae absent from lateral papillae. Setae except for those on lateral papillae ca. as long as spiracular width.

Type material.—*Holotype*: third instar larva, from gall on sugarberry, Waters Dairy Rd., Temple, Texas, IV-28-2010, T.O. Robbins, deposited in USNM.

Etymology.—The name *cornuata* refers to the horn-shaped gall.

Affinities.—This is the only Nearctic *Celticecis* with setose prothoracic sternal papillae in the third instar and without a spatula in the second instar. The Japanese *C. japonica* also has setose sternals on the meso- and metathorax and abdominal segments 1–7, but not on the prothorax, and it has a second instar spatula. That sternal papillae are setose on both species may be only coincidental. The present species has only 2 lateral papillae on each side of the spatula, 2 sternals on the abdominal segments and 4 terminals to *C. japonica*'s 4, 4 and 8, respectively. The third instar spatula of *C. cornuata* has a long spatula shaft unlike the short broad shaft of most other *Celticecis* spp., including *C. japonica*. The closest relative to this species is not apparent, but the lack of a spatula in the second instar might possibly represent the primitive character state for the genus rather than a secondary loss. The prominent callus that remains on the leaf after the gall dehisces is reminiscent of that seen in some stem galling species, e.g., *C. ramicola*.

Biological notes.—Galls were first noticed in Louisiana on March 26 on partially expanded leaves. Galls are usually green when young and turn red with age. Full grown larvae were present in late April in Temple, Texas and in mid to late May in Alexandria and Pineville, Louisiana. Any galls still found attached to the leaves later than May 30 contained either a dead larva or a parasitoid, so the larva had presumably stopped feeding before an abscission layer was formed that would have allowed the galls to dehisce.

Distribution (Map 7).—This species has a southerly U.S. distribution on sugarberry, northern hackberry and dwarf hackberry: **Arkansas**, sugarberry: 4.4 mi. NW Emmet. **Florida**, sugarberry: Fort Pierce, Gainesville, Mims. **Georgia**, dwarf hackberry: Lake Tobesofkee, Bibb Co; Rum Creek Wildlife Management Area, Monroe Co. **Kentucky**, northern hackberry: Cub Run. **Louisiana**, sugarberry: Alexandria, Pineville. **Missouri**, northern hackberry: Columbia. **Texas**, sugarberry: Temple.

Specimens of *C. cornuata* examined.—**Florida**, sugarberry: Paleo Hammock, Fort Pierce, IV-20-10, K.L. Hibbard, 1 second instar. **Kentucky**, northern hackberry: Cub Run, V-27-2011, C. Eiseman, 2 third instars. **Louisiana**, sugarberry: Pineville, Buhlow Lake, VII-24-2010, 1 third instar. **Missouri**, northern hackberry: Columbia, VI-24-1874, C.V. Riley, 1 second instar. **Texas**, sugarberry: Waters Dairy Rd., Temple, IV-28-2010, T.O. Robbins, 1 second and 1 third instar.

Celticecis cupiformis Gagné, new species

Description.—*Gall* (Fig. 18). On leaf lamina, usually on underside of leaf; short-cylindrical, basal margins abruptly rounded, apex broadly rounded and ending in short, central umbo; glabrous, naked or sparsely hairy, the hairs not obscuring surface; green, turning mostly brown, the apex yellow; ca. 1.5 mm high and 1.0 mm wide; connection to leaf circular, flat, ca. 1/3 width of gall base and barely apparent from opposite side of leaf; gall in cross section uniformly thin, brittle, the larval chamber of same shape as gall.

Adult (only female known). Antenna with 12 flagellomeres in female (n=1); third flagellomere diminutive. Wing length: female, 1.5 mm (n=1). **Female abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite quadrate, with single row of posterior setae and no scales; eighth tergite undivided longitudinally, with sparse setae along posterior margin; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high.

Pupa. Unknown.

Larva. **Third instar:** Length, 1.4–1.8 mm (n=8). Pink to red or orange. Body ovoid-spindle-form, weakly sulcate between segments. Spatula (Fig. 131): reduced, the small, acute, anterior tooth nearly as long or longer than poorly defined shaft. Papillae: 4 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic segments, 1 on first through eighth abdominal segments; 4 terminals; 2 sternals on thoracic and abdominal segments; 2 laterals per side, setae not apparent; 1 ventral per side on each segment, with setae, except without seta on eighth abdominal segment. Dorsal, pleural, terminal, and ventral setae shorter than spiracular width. **Second instar**: Length, 0.7 mm (n=1). Spatula (Fig. 155): tooth elongate-acute, longer than apparent shaft. Lateroventral spinules not appreciably larger than elsewhere, but spicules extremely sparse. Dorsal and pleural setae shorter than width of adjacent spiracles, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type material.—*Holotype*: third instar larva, from gall on sugarberry, Georgetown, Texas, VIII-5-2009, RJG.

Etymology.—The name *cupiformis* means "barrel-shaped," with reference to the shape of the gall.

Affinities.—This is a tiny species with only 12 antennal flagellomeres and the larval spatula reduced to a stub in both third and second instars. See under *C. spiniformis* for discussion.

Biological notes.—The gall of this rare species is very tiny, which may explain why it was not collected more often. Full-grown larvae are pink, red, or orange, and completely fill the larval cavity of the gall.

Distribution (Map 8).—This species is known only from southcentral U.S., on sugarberry with the exception of the Belton, Texas collection that was found on both sugarberry and netleaf hackberry growing side by side. It was collected from: **Louisiana**: Alexandria. **Texas**: Belton, Burnet, Georgetown, Luling, Lufkin.

Specimens of *C. cupiformis* examined, all from sugarberry.—**Louisiana**: Alexandria, IV-15-2009, JCM, 1 second instar; VI-20-2001, JCM, 1 third instar. **Texas**: Belton, Miller Springs Nature Area,VIII-4-2009, T.O. Robbins, 2 third instars; Burnet, VIII-5-2009, RJG, 1 third instar; Georgetown, VIII-5-2009, RJG, 1 third instar; Lufkin, X-9-2008, JCM, 3 third instars; Luling, J. Riemann, 1 ♀, emerged III-15-1957.

Celticecis expulsa Gagné, new species

Description.—*Gall* (Figs. 19–21; Plate 2, Fig. 16). On stem, fruit, petiole and base of leaves; irregularly columnar, apically convex or flat, usually with short, central nipple, sometimes 2–3 galls partially coalesced, strongly convex on opposite side of petiole or vein and usually causing leaf distortion; base broad, integral to host tissue, developing apically a circular mark at apex, denoting margin where inner portion of the gall will emerge as a plug from the periphery and dehisce, the remainder of the gall shriveling; green, matte, with sparse white pubescence; 5 mm high, 3 mm broad; the deciduous plug yellow except for green apex, turning brown, larval chamber ovoid, the wall of the plug of uniform thickness

Adult. Antenna with 20 flagellomeres in male (n=1) and 20–23 in female (n=4). Wing length: male, 2.8 mm (n=1); female, 2.9–3.1 mm (n=4). **Male abdomen**: First through seventh tergites with mostly double row of posterior setae laterally, decreasing to one row medially, without lateral setae, and covered with scales; eighth tergite with a few setae apically, pigmented only on anterior half. Terminalia as for *C. celtiphyllia* except gonostylus (Fig. 123) thickest beyond mid-length, setulose except on distal fourth. **Female abdomen** (Fig. 126). First through sixth tergites rectangular, ca. 2× as wide as long, with 3 rows of posterior setae laterally narrowing to one medially and evenly covered with scales; seventh tergite ca. ½ of sixth tergite, quadrate, slightly longer than wide, slightly concave laterally, with 4 rows of posterior setae, scales absent; eighth tergite 1/3 longer than seventh tergite, completely divided longitudinally and resulting in two narrow sclerites with scattered tiny setae at posterior end of each; ovipositor elongate-protrusible; ninth segment to end of fused cerci 0.94–1.06 mm long and 3.7–3.9 times as long as sixth tergite (n=4); cerci elongate-cylindrical.

Pupa (Figs. 85–86). Antennal bases bilaterally compressed, keel-like ventrally, diverging and pointed apically, acutely triangular in lateral view. Face with pair of protuberances.

Larva. **Third instar**: White. Length, 2.2–3.5 (n=8). Body spindle-form, as thick as broad at

middle. Spatula (Fig. 133): with large quadrate shaft and two acute anterior teeth, the teeth separated from one another by ca. the length of their basal width, with a short convexity between them. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals per side on all thoracic and abdominal segments; 8 terminals; 2 sternals on thoracic and 4 on abdominal segments; laterals 2 per side with barely apparent setae; ventrals 1 per side on each segment except 2 per side on eighth abdominal segment, all with setae. Dorsal, pleural, ventral and terminal setae as long as width of spiracles. **Second instar** (Fig. 156): White. Length, 1.2–2.2 (n=7). Spindle-form. Spatula (Fig. 156): triangular with single, acute anterior tooth, shaft as narrow as base of tooth anteriorly and spreading posteriorly. Ventral spinules more diminutive than those on dorsum but not appreciably larger on thorax than on abdomen. Papillae as for third instar except ventrals on eighth abdominal segment with setae variable in length or not apparent.

Type material.—*Holotype:* female, from galls collected VI-5-2009 on northern hackberry, Lawrence, Kansas, G.-S. Tung, emerged III-16-2011, deposited in USNM.

Etymology.—The name *expulsa*, meaning forced out, refers to the separation of the hard plug bearing the larval chamber from the remaining persistent part of the gall.

Affinities.—This species and *C. celtiphyllia* have the longest ovipositors in *Celticecis* and are the only two species with the female eighth abdominal tergite completely divided longitudinally. Nevertheless, *C. expulsa* appears to be more closely related to *C. connata*. The two share the complete lack of lateral setae on the abdominal tergites and the distally widened gonostylus.

Biological notes.—The gall of this species is the only one in North America that is not entirely detachable. Initially it appears as a simple columnar elevation of the plant tissue but eventually the interior of the gall surrounding the larval chamber separates as a distinct, hard, cylindrical core (Fig. 21). In due course the outer tissue shrivels, allowing the core to drop to the soil. In Alexandria, Louisiana, and Holland, Texas, galls were evident in early April, already with second instars. Most galls had dehisced by mid-May wherever the gall was found. Adults were reared in March and April, 2011, from galls taken in June, 2009, in Lawrence, Kansas.

The parasitoids *Gastrancistrus* sp. and *Trichacis* sp. from Alexandria, Louisiana were reared in spring from galls collected the previous summer, and a different *Gastrancistrus* sp. from Lawrence, Kansas was reared in 2011 from galls collected in 2009.

Distribution (Map 9).—Galls were found on both northern hackberry and sugarberry. This species may be more widespread than the distribution list indicates, but galls develop and excise earlier in the season than most of our collections were made. **Kansas**, northern hackberry: Lawrence. **Kentucky**, northern hackberry: Lexington. **Louisiana**, sugarberry: Alexandria. **Maryland**, northern hackberry: Cabin John, Poolesville. **Texas**, sugarberry: Holland, Temple. **West Virginia**, northern hackberry: Falling Waters, 6 mi. NW Hedgesville.

Specimens of *C. expulsa* examined : **Kansas**, northern hackberry: Lawrence, VI-5-2009, G.-S. Tung, 1 ♂, 4 ♀, emerged III-16 to IV-10-2011. **Kentucky**, northern hackberry: Lexington, V-25-2009, L. Rieske, 2 third instars. **Louisiana**, sugarberry: Alexandria, IV-19-2009, JCM, 4 second instars. **Maryland**, northern hackberry: Cabin John, V-12-2009, RJG, 4 second instars; V-14-2009, RJG, 2 second and 4 third instars. **Texas**, sugarberry: Waters Dairy Rd, Temple, IV-27-2010, T.O. Robbins, 2 second and 1 third instars. **West Virginia**, northern hackberry: Falling Waters , V-24-2009, 3 third instars, RJG.

Celticecis globosa Gagné, new species

Cecidomyia sp. Wells 1916: 273, Plate XVII, Fig.12a.

Description.—*Gall* (Figs. 22–23, 40; Plate 1, Figs. 12–12a). Attached to leaf vein, usually on underside of leaf; ovate to globular, upright, often with lateral or encircling bulge near mid-length, apex flattened; light green, white to yellow, turning reddish, matte, naked or, in most specimens from southcentral U.S. (Arkansas, Louisiana, Mississippi and Texas) covered with short pubescence not obscuring surface; ca. 3.0–3.5 mm long and 2.0–2.5 mm wide; apparent on opposite side of leaf as minute convexity; wall uniformly thin except at bulge when present, larval chamber ovate, shaped as for gall not including bulge.

Adult. Antenna with 18 flagellomeres in male (n=1) and 17–18 in female (n=4). Wing length:

male, 2.1–2.9 mm (n=5); female, 2.3–2.4 mm (n=5). **Male abdomen**: First through sixth tergites rectangular, with mostly single row of posterior setae, without lateral setae, elsewhere covered with scales; seventh tergite rectangular, with double row of posterior setae intermixed with scales that extend in coverage only slightly anterior to setal row; eighth tergite weakly sclerotized, with row of short setae on the posterior, unpigmented edge of the sclerite. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites with single row of posterior setae, without lateral setae, and covered with scales; seventh tergite ca. ½ width of sixth tergite, quadrate, with 2 rows of posterior setae, with scales barely extending anteriad of posterior setae; eighth tergite quadrate, subequal in length to seventh but narrower, undivided longitudinally, with double row of tiny setae along posterior margin; cerci bulbous, ca. as long as high. Ninth segment to end of fused cerci 0.45–0.55 mm long and 2.4–2.7 times as long as length of sixth tergite (n=5).

Pupa (Figs. 87–88). Antennal bases dorsoventrally flattened, thin and tapered in lateral view, broad and apically rounded in ventral view, adjacent almost to apex. Face without protuberances.

Larva. **Third instar**: Length, 2.4–3.1 mm (n=10). White to yellow. Body generally spindleform but slightly broader than thick, deeply sulcate between segments. Spatula (Fig. 137): with large shaft, divided anteriorly basad of the short, widely separated, acute anterior teeth, not extending appreciably laterad of teeth. Papillae: 4 dorsals on thorax, 6 on first through seventh abdominal segments, and 2 on eighth abdominal; 2 pleurals on each side on all segments; 6 terminals, occasionally 5 or 8; 2 sternals on thoracic and abdominal segments; 2 laterals per side with short setae, only slightly longer than papillar base; 1 ventral per side on each segment, with seta, the 2 per side on eighth abdominal segment with or without setae. Dorsal, pleural, and terminal setae ca. as long as spiracular width, the ventrals slightly shorter. **Second instar**: Length, 0.9–1.6 (n=10). Spatula (Fig. 159): with acute anterior tooth approximately as long and 1/2 as wide as shaft. Lateroventral spinules not larger on thorax than elsewhere. Dorsal, pleural, terminal and ventral setae ca. 1 ½ times as long as spiracular width.

Type material.—*Holotype*: female, northern hackberry, IX-1-2008, Lawrenceburg, Kentucky, RJG, emerged IV-19-2009, deposited in USNM.

Etymology.– The name *globosa* refers to the spheroid shape of the gall.

Affinities.—See discussion under *C. pubescens*.

Biological notes.—The gall exterior is naked (Fig. 22) or, in most specimens from Arkansas, Louisiana, Mississippi and Texas, fuzzy (Fig. 40). At the beginning of our study we kept these separate, but in the end we could find no other distinction between specimens of *C. globosa* from the hairy and non-hairy galls. This gall appears generally late in the season. In Alexandria, Louisiana, we noticed young galls with already developed second instars only in early July. These continued to develop long after galls of all other species except some *C. pubescens* were all mature. As late as September 25, some galls of *C. globosa* still contained second instars, although most contained third instars. By mid-October almost all galls contained third instars. Galls with viable third instars were still common on leaves on November 20, long after galls of most other species remaining on the leaves contained only dead larvae or parasitoids. In Kentucky, Ohio and Maryland, galls of *C. globosa* were also late, making it the most common gall collected in August and September. Larvae are usually white but some turn yellow to orange.

Trichacis sp. near *texana* Fouts was reared in spring from galls of *C. conica* collected the previous summer at Cabin John, Maryland. *Tenuipetiolus* sp. and *Torymus* sp. near *tubicola* (Osten Sacken) were reared in spring from galls collected the previous summer from Alexandria, Louisiana.

Distribution (Map 10).—This is a widespread species in eastern U.S. on both northern hackberry and sugarberry. Galls are known from: **Arkansas**, sugarberry: 4.4 mi. NW Emmet. **Florida**, sugarberry: Gainesville. **Iowa**, northern hackberry: Ames, Lansing. **Kansas**, northern hackberry: Lawrence. **Kentucky**, northern hackberry: Georgetown, Lawrenceburg, Lexington. **Louisiana**, sugarberry: Alexandria, New Orleans, Pineville. **Maryland**, northern hackberry: Cabin John, Hancock, Lanham, Williamsport, Wittman. **Mississippi**, sugarberry: Greenville, Grenada, Stoneville. **Ohio**, northern hackberry: Ashville, Batavia, Columbus, Union. **Texas**, sugarberry: College Station, Donie, Lufkin, Marlin, Nacogdoches. **West Virginia**, northern hackberry: Cherry Run, Falling Waters, 6 mi. NW Hedgesville, Paw Paw.

Specimens of *C. globosa* examined: **Arkansas,** sugarberry: NW Emmet, VIII-20-2009, T.O. Robbins, 1 second and 1 third instar. **Iowa**, northern

hackberry: Ames, IX-27-2010, M.J. Hatfield, 2 third instars. **Florida**, sugarberry: Gainesville, VI-21-2011, J. Brambila, 1 third instar. **Kansas**, northern hackberry: Lawrence, VI-5-2009, G.-S. Tung, 3 second instars. **Kentucky**, northern hackberry: Lawrenceburg, IX-1-2008, RJG, 6 third instars and 1 ♂, 7 ♀, and 4 pupae, emerged IV-18–19, 2009. **Louisiana**, sugarberry: Alexandria: X-21-2008, JCM, 2 third instars; VIII-1-2010, JCM, 3 second and 1 third instars; VIII-15-2010, JCM, 2 third instars; VIII-22-2010, JCM, 2 third instars and 10 ♂, 15 ♀ and 5 pupae, emerged III-5 to IV-7-2011; IX-26-2010, JCM, 3 third instars; X-3-2010, JCM, 5 third instars; VIII-7-2011, JCM, 2 second and 1 third instars; Pineville, X-4-2008, JCM, 3 second and 2 third instars. **Maryland**, northern hackberry: Cabin John, VII-22-2010, RJG, 2 third instars; Hancock, IX-11-2008, RJG, 2 third instars; Hancock, IX-11-2010, RJG, 3 third instars; Wittman, VII-5-2009, RJG, 1 second and 1 third instars. **Mississippi**, sugarberry: Grenada, IX-2-2008, RJG, 2 third instars; Stoneville, IX-5-2008, RJG, 1 third instar. **Ohio**, northern hackberry: Ashville, VII-20-2011, RJG, 2 second instars. **Texas**, sugarberry: College Station, VIII-3-2009, RJG, 3 third instars; Donie, VIII-21-2009, T.O. Robbins, 1 second and 3 third instars; Kurth Lake, near Lufkin, X-9-2008, JCM, 1 third instar; Kurth Lake, near Lufkin, X-22-2009, JCM, 3 third instars; Marlin, VIII-21-2009, T.O. Robbins, 1 third instar. **West Virginia**, northern hackberry: Cherry Run, VIII-7-2010, RJG, 1 third instar; Falling Waters, VI-14-2009, RJG, 2 second instars; 6 mi. NW Hedgesville, VIII-30-2009, RJG, 2 third instars.

Celticecis ovata Gagné, new species

Description.—*Gall* (Fig. 24). On twigs, petioles or major veins of either leaf surface and often distorting the leaf, usually in crowded clusters; bulbous basally, the distal 1/3–2/3 gradually tapering to apex; connection to twig a pad as wide as gall base; surface green, turning brown, the surface then weakly longitudinally sulcate along entire length; covered with long white hair not obscuring surface; 5–6 mm long and 4–5 mm at widest diameter; wall woody, uniformly thick or thin, larval chamber of same shape as spheroid part of gall, not extending into tapered apical portion.

Adult, pupa. Unknown.

Larva. **Third instar**: Length, 2.9–3.5 mm (n=5). Yellow. Body widest at middle, tapering to ends, broader than thick, moderately furrowed between segments. Spatula (Fig. 138): with two acute, nearly equilateral anterior teeth separated from one another by less than the distance between them, the large shaft generally quadrate. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals per side on all thoracic and first through eighth abdominal segments; 8 terminals; 2 sternals on thoracic segments, 4 on first through eighth abdominal segments; 2 laterals per side usually with prominent setae nearly as long as setae on adjacent ventral papillae, and occasionally a third papilla without seta; 1 setose ventral per side except eighth abdominal segment with 4, usually with setae, occasionally 1 or 2 without. Dorsal and pleural setae of eighth abdominal segment ca. 1½ times as long as width of adjacent spiracle and subequal to terminal setae. **Second instar**: Length, 1.3–1.4 mm (n=8). Spatula (Fig. 160): more or less triangular, anterior tooth nearly equilateral, less than 1/3 length of shaft; shaft widening gradually from base of tooth to broad posterior limit. Body evenly covered with spinules, lateroventral spinules not larger on thorax than elsewhere. Dorsal and pleural terminal setae of eighth abdominal segment 1½ times longer than spiracular width and subequal to terminal setae.

Type material.—*Holotype*: third instar larva, VI-3-2009, Cabin John, Maryland, RJG, deposited in USNM.

Etymology.—The name *ovata* refers to the general shape of the mature gall.

Affinities.—See under *C. semenrumicis*.

Biological notes.—The generally globular gall base becomes longitudinally sulcate when dried, lending the galls some slight resemblance to those of *C. semenrumicis*. Young galls are similar to those of *C. celtiphyllia*, but those of the latter species eventually broaden apically and, when dry, may develop longitudinal sulcations only on the basal half.

Distribution (Map 11).—This species was mainly found on northern hackberry but was found in southeastern Virginia on both northern hackberry and sugarberry growing next to one another and in Georgia on dwarf hackberry. Galls were collected from: **Georgia**, dwarf hackberry: Rum Creek Wildlife Management Area, Monroe Co., L. Tobesofkee, Bibb Co. **Iowa**, northern hackberry: Cedar Rapids. **Kentucky**, northern hackberry: Lexington. **Maryland**, northern hackberry: Cabin John, Potomac. **Ohio**, northern hackberry:

Ashville, Cincinnati, Columbus. **Virginia**, northern hackberry and sugarberry: Suffolk. **West Virginia**, northern hackberry: 6 mi NW Hedgesville. **Wisconsin**, northern hackberry: Cross Plains.

Specimens of *C. ovata* examined (all on northern hackberry except Georgia specimens on dwarf hackberry).— **Georgia**, dwarf hackberry: Rum Creek Wildlife Management Area, Monroe Co., VI-6-2011, J. & R. Payne, 3 second instars. **Iowa**, northern hackberry: Cedar Rapids, VI-16-2011, J. Zito, 4 second instars. **Maryland**, northern hackberry: Potomac, VI-7-1984; Cabin John, V-8-1985, RJG, 3 second instars; Cabin John, V-12-2009, RJG, 2 second instars; Cabin John, VI-3-2009, RJG, 3 second and 1 third instars; Cabin John, VI-5-2011, RJG, 3 second instars. **Ohio**, northern hackberry: Ashville, VII-20-2011, RJG, 2 second instars. **Virginia**, northern hackberry: Suffolk, VI-16-2010, RJG, 2 second and 1 third instars. **West Virginia**, northern hackberry: 6 mi NW Hedgesville, IX-12-2008, RJG, 2 second and 1 third instars.

Celticecis oviformis (Patton)

oviformis Patton 1897: 248 (*Cecidomyiaceltis*), with reference to gall #30 of Riley 1890: 612; *Cecidomyia* sp., Wells 1916: 274, Plate XVIII, Figs. 14, 14a; Felt 1918: 124 (erroneously as syn. of *Phytophaga celtiphyllia*); Felt 1940: Plate 40, Fig 5. misidentified as *Phytophaga celtiphyllia;* Gagné 1983: 437 (*Celticecis*).

Description.—*Gall* (Figs. 25–27; Plate 2, Figs. 14, 14a). Usually along twig, occasionally on petiole or major veins of upper side of leaf, most often in groups; evenly spherical beyond obtuse, often weakly lobed base, with short apical nipple; green, turning brown, uniformly short-fuzzy but hairs not obscuring matte surface; 5–6 mm long, 4–5 wide; connection to host a prominent, circular, flat, persistent brown callus nearly 1/2 as wide as gall base; when on leaf apparent on opposite side of leaf as a thickening of vein; wall of uniform thickness throughout, larval chamber spherical, of same shape as gall.

Adult (female only).—Antenna with 22–23 flagellomeres (n=2). Wing length: 3.4–4.5 mm (n=4). **Female abdomen**: First through sixth tergites rectangular, ca. 2× as wide as long, with 3 rows of posterior setae laterally, soon narrowing to one row, then setae absent medially, scales extremely sparse or absent; seventh tergite ca. ½ width of sixth tergite, quadrate, slightly longer than wide, with 4 rows of posterior setae laterally narrowing to 2 medially, scales absent; eighth tergite as long as but narrower than seventh tergite, anterior edge deeply concave, with several rows of short setae posteriorly; ovipositor elongate-protrusible; cerci ovoid-cylindrical, ca. 3× as long as high. Ninth segment to end of fused cerci 0.90–0.93 mm long and 2.5–2.6 times as long as length of sixth tergite (n=4).

Pupa. As for *C. connata* (Figs. 83–84) but without facial protuberances. Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, diverging only apically, acutely triangular in lateral view.

Larva. **Third instar**: Length, 4.5–6.2 mm (n=6). White. Body spindle-form, sulcate between segments. Spatula (Fig. 139): with large quadrate shaft except for concavity between the two widely separated, acute anterior teeth, the teeth separated from one another by ca. the length of their basal width. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals per side on all thoracic and abdominal segments; 8 terminals; 2 sternals on thoracic and 4 on abdominal segments; laterals 2 per side with barely apparent setae, no longer than width of papillar base; ventrals 1 per side on each segment, with seta, except 2 per side on eighth abdominal segment, both with setae. Dorsal, pleural, terminal, and ventral setae 1/3–1/2 longer than spiracular width. **Second instar**: Length, 1.6–2.4 mm (n=7). Spatula (Fig. 161): with ovoid shaft and narrow, acute anterior tooth. Length of papillae with same proportions as for third instar.

Type material.—*Lectotype*: gall, **here designated**, from northern hackberry, Columbia, Missouri, VI-24-1874, 106L, deposited in USNM. A second instar larva was retrieved from the lectotype gall and placed on a slide labeled as being from the lectotype gall. Paralectotypes, 11 galls, eight belonging to *C. oviformis*, the remainder to *C. connata*. As Riley (1890) suspected, his series included two kinds of galls. The entire series was originally labeled only as "106L." This code was traced to an old Department of Agriculture card file where the more specific collection data were found.

Etymology.—Patton (1897) evidently coined the name *oviformis* following Riley's (1890) obser-

vation that the galls resembled the large eggs of a diurnal lepidopteran.

Affinities.—This species is unique for the genus in that the female abdominal tergites lack scales, the eighth tergite is no longer than the seventh but has a deeply concave anterior edge, and the cerci, while about 3× as long as high, are appreciably broader than those of other *Celticecis* spp. with long cerci. Unfortunately, the male is unknown. It would have been interesting to compare its gonostyli with the peculiar ones of *C. connata* and *C. expulsa*.

Biological notes.—Galls of this species have a similar shape to those of *C. connata* when those of the latter are not found in aggregate, but galls of *C. oviformis* are covered with fine pubescence and are uniformly thin-walled, unlike galls of *C. connata* that are hairless and have thick walls of irregular diameter. Galls of *C. oviformis* develop and dehisce early in the season, possibly why it was not collected more often. In mid-April when galls were first noticed in Alexandria, Louisiana, they already contained second instars. After mid-May galls of this species still found attached to the host were parasitized.

Gastrancistrus sp. was reared in spring from galls of *C. oviformis* collected the previous summer in Lawrence, Kansas. *Torymus* sp. near *tubicola* (Osten Sacken) was reared the same summer that the galls were collected at Cabin John, Maryland.

Distribution (Map 12).—This species is widespread in the U.S. and found on both northern hackberry and sugarberry. Galls are known from: **Florida**, sugarberry: Basinger. **Illinois**, northern hackberry: Peoria. **Kansas**, northern hackberry: Lawrence. **Louisiana**, sugarberry: Alexandria, Pineville. **Maryland**, northern hackberry: Cabin John, Poolesville, Potomac. **Missouri**, northern hackberry: Columbia. **Ohio**, northern hackberry: Columbus. **West Virginia**, northern hackberry: Falling Waters. **Texas**, sugarberry: Holland.

Specimens of *C. oviformis* examined.—**Kansas**, northern hackberry: Lawrence, VI-5-2009, G.-S. Tung, 4 third instars, and 2 ♀ and 2 pupal exuviae, emerged III-19 to IV-15-2010. **Louisiana**, sugarberry: Alexandria, IV-19-2009, JCM, 2 third instars; Alexandria, IV-25-2009, 4 third instars. **Maryland,** northern hackberry: Cabin John, V-3-2009, RJG, second instar; Cabin John, V-7-2009, RJG, 1 second and 4 third instars; VI-3-2009, RJG, 2 third instars, and 2 ♀ and 1 pupal exuviae, emerged IV-15-2010. **Missouri**, northern hackberry: Columbia, IV-24-1874, C.V. Riley, 2 second instars, including topotype.

Celticecis pilosa Gagné, new species

Description.—*Gall* (Fig. 28). On leaf lamina on underside of leaf, usually in groups; upright-conical, apex pointed, base circular, not flared; surface covered with white hair nearly obscuring green surface; 3.5–4.5 mm high and 2.0–3.0 mm wide at base; connection to leaf circular, flat, ca. 1/3 width of gall base; apparent on opposite side of leaf as slight, sometimes discolored convexity; gall in cross section thickest near base surrounding larval chamber, thinning and less woody and more brittle apically.

Adult, pupa. Unknown.

Larva. **Third instar**: Length, 2.0–2.2 mm (n=2). Body elongate-ovoid, only slightly sulcate intersegmentally; anterior and posterior ends blunt except for pointed head. Spatula (Fig. 140): with 2 anterior teeth and ovoid shaft. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 4 terminals; 2 sternals on thoracic and first through seventh abdominal segments; 2 laterals per side of midline, setae if apparent shorter than socket diameter; 1 ventral per side on each thoracic and first through eighth abdominal segments, that of eighth abdominal segment lacking the seta. All papillar setae except those of laterals ca. as long as spiracular width. **Second instar**: Length 1.0–1.4 mm (n=8). Spatula (Fig. 162): with 1 or 2 acute teeth, closely approximated if 2 teeth, ca. 1/3 as long as shaft, shaft broad, indented laterally at mid-length. Latero-ventral spinules appreciably larger on thorax than on abdomen. Dorsal, pleural and terminal setae longer than spiracular width, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type-material.—*Holotype*: third instar larva, *Celtis occidentalis*, Winchester, Kentucky, VI-23-2010, RJG, deposited in USNM.

Etymology.—The name *pilosa* refers to the hairy gall covering.

Affinities.—This is the only *Celticecis* species with usually two teeth on the second instar spatula. With either one or two teeth, the spatula

resembles in general shape and large size of that of *C. subulata*, the main difference being the much larger tooth on *C. subulata*. See under *C. spiniformis* for further discussion.

Distribution (Map. 13).—This species was the most rarely collected species of *Celticecis*. It was found only on northern hackberry: **Kentucky**: Georgetown, Lexington, Winchester.

Specimens of *C. pilosa* examined.—K**entucky**: Georgetown, VI-23-2010, RJG, 1 second instar; Lexington, V-28-2009, L. Rieske, 5 second instars; Winchester, VI-23-2010, RJG, 2 second and 2 third instars.

Celticecis pubescens (Patton)

pubescens Patton 1897: 248 (*Cecidomyiaceltis*), with reference to gall #32 of Riley 1890: 613; Felt 1918: 123 (*Cecidomyia*); Felt 1940: 233, Plate 40, Fig. 9 (*Cecidomyia*); Gagné 1983: 437 (*Celticecis*).

texana Felt 1935: 8 (*Phytophaga*); Painter 1935: 87, Plate 2, Fig. 5 (*Phytophaga*); Felt 1940: 234 (*Phytophaga*); Gagné 1983: 437 (*Celticecis*). **New synonym**.

Description.—*Gall* (Figs. 29–30). On underside of leaf, in vein fork, occasionally two adjacent in a fork and then sometimes partly or wholly coalesced, usually perpendicular to leaf; stout-cylindrical with short apical tubercle in center of flattened apex and base abruptly tapering to short peduncle; surface green, turning brown, with or without long white pubescence that may sometimes obscure surface; ca. 4 mm long and 3 mm in diameter; apparent on opposite side of leaf as slight, sometimes discolored convexity; walls in cross section thick, yellowish, woody, larval chamber elongate-ovoid, nearly as long as gall.

Adult. Antenna with 16–17 flagellomeres in male (n=5) and female (n=5). Wing length: male, 2.5–2.8 mm (n=5); female, 2.1–2.7 mm (n=5). **Male abdomen**: First through sixth tergites rectangular, with mostly single row of posterior setae, without lateral setae, elsewhere covered with scales; seventh tergite rectangular, with double row of posterior setae intermixed with scales extending in coverage only slightly anteriad of posterior setae; eighth tergite weakly sclerotized, without vestiture except for anterior pair of trichoid sensilla. Terminalia as for *C. celtiphyllia* (Figs.119–120) **Female abdomen**: First through fifth tergites as for male; sixth tergite rectangular with 2 rows of posterior setae and elsewhere covered evenly with scales; seventh tergite ca. 1/2 width of sixth tergite, quadrate, slightly wider than long, with 2–3 rows of posterior setae and scattered scales on posterior half; eighth tergite quadrate, as long as and slightly narrower than previous tergite, undivided longitudinally, with 2 rows of short setae along posterior margin; ovipositor elongate-protrusible; cerci short, spheroidal, as long as high. Ninth segment to end of fused cerci 0.52–0.55 mm long and 2.8–3.1 times as long as length of sixth tergite (n=4).

Pupa (Figs. 89–90). Antennal bases closely appressed except separated apically, the apices dorsoventrally compressed. Face without protuberances.

Larva. **Third instar**: Length, 2.0–2.8 mm (n=8). White to yellow. Body spindle-form, slightly sulcate intersegmentally, the anterior and posterior ends blunt except for pointed head. Spatula (Fig. 141): with large quadrate shaft not extending appreciably laterad of anterior teeth, the teeth acute, relatively short, separated from one another by approximate basal width of one tooth. Papillae: 4 dorsals on thorax, 6 on first through seventh abdominal segments and 2 on eighth abdominal; 2 pleurals each side on thoracic segments and eighth abdominal, one each on first through seventh abdominal segments; usually 6 terminals, occasionally 5 or 4; 2 sternals on thoracic, 4 on abdominal segments; 2, rarely 3, laterals per side with setae apparent, long to short; 1 ventral per side on each segment, with seta, except 2 on eighth abdominal segment, without setae. All setae except laterals approximately as long as 2/3 width of spiracles. **Second instar**: Length, 0.9–1.2 mm (n=7). Spatula (Fig. 163): with acute, anterior tooth less than 1/2 as long and wide as quadrate shaft. Ventral spinules more diminutive than those on dorsum but not appreciably larger on thorax than on abdomen. Papillae as for third instar. Setae except for laterals not longer than width of spiracles.

Type material.—*Cecidomyiaceltis pubescens* Patton: *Syntypes:* 4 galls, 2 each on a section of leaf on separate pins. The label on each pin reads: "Cecid on *Celtis texana*[,] Columbus[,] Tex[,] 7/17/79[, C.V.] Riley." Deposited in USNM.

Phytophaga texana Felt: *Holotype*: male, reared from gall on reticulate hackberry, collected at Austin, Texas, VII-10-1922, R.H. Painter #45, 13308, deposited in NYSM. This name is synonymized here because the figure of the gall given in Painter (1935: Plate 2, Fig. 5) is similar to those of *C. pu-*

bescens, and the holotype and a female and larva associated with it conform to larvae taken and adults reared from galls typical of *C. pubescens*.

Etymology.—The name *pubescens* refers to the hairy covering of the gall.

Affinities.—This species and two others, *C. pyriformis* and *C. wellsi*, appear to be related. All three cause upright, columnar, woody, more or less hairy leaf galls that are attached to veins, have only four instead of the primitive six dorsal papillae on the larval thoracic segments, one instead of two pleural setae on each side of the first through seventh abdominal segments, and *C. pubescens* and *C. wellsi* share the foreshortened female fused cerci that are no longer than high. The female of *C. pyriformis* is still unknown. *Celticecis globosa* may also be related to these three. It shares the short female cerci and the reduced number of four dorsal papillae on the larval thorax, but has the full complement of two pleural papillae on each side the abdominal segments. The gall of *C. globosa* is also upright and woody but the larval chamber is ovoid instead of columnar and the larva itself is flatter and more deeply sulcate between segments.

Biological notes.—Young galls of this species bearing second instars were seen in late April and mid-May in Louisiana, but young, soft galls continued to appear through July. Galls with full-grown larvae are commonly found in August but some still contain second instars. Full-grown larvae are yellow to orange and fill the larval chamber. Persistent galls found later than August are generally parasitized; many galls of the current season can be found with a parasitoid's exit hole at the very base of the gall. Adult *C. pubescens* were reared in spring of 2010 and 2011 from galls collected in summer of 2009 in Temple, Texas.

Several parasitoids were reared in spring from galls of *C. pubescens* collected the previous summer: *Gastrancistrus* sp., *Platygaster* sp. and *Trichacis mandibulata* Masner from Mims, Florida, and *Torymus* sp. near *diabolus* Moser from Georgetown, Texas.

Distribution (Map 14).—This is a southern U.S. species known from Florida to Arizona and found on sugarberry, netleaf hackberry and northern hackberry. **Arizona**, netleaf hackberry: Camp Verde and Sycamore Canyon Wilderness. **Arkansas**, sugarberry and northern hackberry: 4.4 mi. NW Emmet, Searcy. **Florida**, sugarberry: Edgewater, Fort Pierce, Gainesville, Glencoe, Mims, Williston. **Louisiana**, sugarberry: Alexandria, Pineville. **Texas**, sugarberry and also netleaf hackberry at Belton: Austin, Belton, Bertram, Burnet, College Station, Columbus, Donie, Georgetown, Lubbock, Lufkin, Luling, Marlin, Nacogdoches, Temple.

Specimens of *C. pubescens* examined.—**Arizona**, netleaf hackberry: Sycamore Canyon Wilderness, VII-11-2009, R. Fitzgibbon and B. Geils, 2 second instars; Sycamore Canyon Wilderness, VIII-27-2010, R. Fitzgibbon, 2 third instars. **Arkansas**, sugarberry: 4.4 mi. NW Emmet, VIII-20-2009, T.O. Robbins, 2 third instars. **Florida**, sugarberry: Edgewater, VI-26-2009, K.L. Hibbard, 2 third instars; Fort Pierce, IV-29-2009, K.L. Hibbard, 5 third instars; Mims, VI-27-2010, K. Hibbard, 1 second and 1 third instars, and 3 ♀, 3 pupae, emerged III-22-2011. **Louisiana**, sugarberry: Alexandria, VI-21-2009, JCM, 4 second and 4 third instars; Alexandria, VII-16-2009, JCM, 2 second and 1 third instars; Alexandria, VIII-8-2009, JCM, 2 ♀, 2 pupae, emerged IV-24-2010; Pineville, VI-24-2009, JCM and R. Fitzgibbon, 2 second instars. **Texas**, sugarberry: Austin, holotype of *Phytophaga texana*; Belton, VIII-4-2009, T.O. Robbins & RJG, 1 second and 1 third instars; Burnet, VIII-5-2009, RJG, 1 third instar; College Station, VIII-3-2009, 1 third instar; Columbus, VII-17-1879, C.V. Riley, 1 third instar; Donie, VIII-21-2009, T.O. Robbins, 1 third instar; Luling, 1956, J. Riemann, 1 ♂, 4 ♀, emerged II-23-1956; Temple, 2 third instars, 5 ♂, 12 ♀ and 3 pupae, emerged III-17 to IV-10-2010, and 1 ♂ and 5 ♀, emerged III-20 to 25-2011.

Celticecis pyriformis Gagné, new species

Unnamed species, Riley 1890: 614 (as number 35); unnamed, Sears 1914: 384, Fig. 35; *Cecidomyia* sp., Wells 1916: 274, Plate XVII, Figs. 13, 13a.

Description.—*Gall* (Figs. 31–32; Plate 1, Figs. 13, 13a–b). Attached singly or serially to more prominent leaf veins on underside of leaf, occasionally adjacent galls partially fused; generally cylindrical, becoming bulbous at base, upright to recumbent, apex flat except for short central nipple; green turning yellow, sparsely to densely covered with long, crinkly white hair of variable length; 3–4 mm long and 2–3 mm broad at base; connection to vein conspicuous, often causing swelling of vein nearby and appearing as a convexity on opposite side of leaf; mature gall in cross section woody, wall of uniform thickness or

thickest basally and thinning beyond mid-length, larval chamber elongate ovoid, nearly as long as gall.

Adult and pupa. Unknown.

Larva. **Third instar**: Length 2.2–2.8 mm (n=7). Yellow. Body spindle-form, slightly sulcate intersegmentally, the anterior and posterior ends blunt except for pointed head. Spatula (Fig. 142): shaft generally quadrate, the long, acute, anterior teeth set well apart and ca. 1/2 the length of shaft. Papillae: 4 dorsals on thorax, 6 on first through seventh abdominal segments, 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; usually 6 terminals, occasionally 4 or 5; 2 sternals on thoracic and 4 on first through seventh abdominal segments; 2 laterals per side, their setae longer than base of papilla; 1 ventral per side on each thoracic and first through seventh abdominal segments with seta, 2 on eighth abdominal segment and lacking the seta. Dorsal, pleural, and terminal setae ca. as long as spiracular width, the ventrals ca. 1/2 as long. **Second instar**: Length, 0.9–1.2 mm (n=5). Yellow. Spatula (Fig. 164): with almost equilateral tooth and large shaft more than 2× as wide and 2× as long as tooth. Lateroventral spinules not appreciably larger on thorax than on abdomen. Dorsal, pleural, and terminal setae ca. as long as spiracular width, the laterals somewhat shorter, especially on thorax.

Etymology.—The name *pyriformis* means "pear-shaped," with reference to the shape of the mature gall.

Type material.—*Holotype*: third instar larva, from gall on northern hackberry, Cabin John, Maryland, VII-7-2008, RJG, deposited in USNM.

Affinities.—See discussion under *C. pubescens*.

Biological notes.—In Maryland galls were first found in early June already with yellow second instars. By mid-July some galls contained either second or third instars and in mid-August larvae were in the third instar and the larval chambers were lined with silk. Once, at Falling Waters, West Virginia, a gall contained a predaceous *Lestodiplosis* larva feeding on the *C. pyriformis* larva. A hole was present at the base of the gall, but it is doubtful that the *Lestodiplosis* made the hole.

Distribution (Map 15).—This species is known only from northern hackberry and has a northerly U.S. distribution, from Kansas to Maryland: **Kansas**: Lawrence. **Kentucky**: Georgetown, Winchester. **Illinois**: Peoria. **Maryland**: Cabin John, Hancock, Poolesville, Williamsport. **Missouri**: Columbia. **Ohio**: Ashville, Batavia, Columbus, Sandusky. **West Virginia**: 6 mi. NW Hedgesville, Falling Waters, Paw Paw.

Specimens of *C. pyriformis* examined (all from northern hackberry).—**Kentucky**: Winchester, VI-23-2010, RJG, 2 third and 1 second instars. **Maryland**: Cabin John, VIII-7-2008, RJG, 1 third instar; Hancock, VII-5-2009, 1 third and 2 second instars. **Missouri**: Columbia, VI- 24-1874, C.V. Riley, 2 second and 5 third instars. **Ohio**: Ashville, VII-20-2011, RJG, 2 second instars; Batavia, VII-20-2011, RJG, 1 third instar. **West Virginia**: 6 mi. NW Hedgesville, VIII-30-2009, RJG, 1 third instar; Falling Waters, VI-30-2010, RJG, 2 third instars.

Celticecis ramicola Gagné, new species

Description.—*Gall* (Figs. 33–35). Usually on stem, occasionally on petiole or base of leaf and then often crowded and distorting leaf; closely placed galls may be partially connate; cylindrical or subcylindrical, abruptly tapering distally to narrow, elongate apex; connection to plant as wide as gall, apparent on other side when on leaf as a conspicuous convexity; hairless, granulose, may be weakly furrowed longitudinally, green, eventually turning brown; 3.0–4.0 mm high, ca. 2.5 mm in diameter; wall eventually woody, uniformly thin throughout, larval chamber of same shape as gall.

Adult. Antenna with 16–17 flagellomeres in male (n=3) and 17 in female (n=2). Wing length: male, 2.5–2.6 mm (n=3); female, 2.6 mm (n=1). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with double row of posterior setae intermixed with scales that cover posterior 2/3 of sclerite; eighth tergite weakly sclerotized beyond anterior pair of trichoid sensilla, with single row of sparse posterior setae and no scales along posterior margin. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites with 1–2 rows of posterior setae except sixth with 2 rows, without lateral setae, and covered with scales; seventh less than 1/2 width of sixth tergite, quadrate, slightly wider than long, with 2–3 rows of posterior setae, scales only poste-

riorly; two separate pigmented areas extend from posterior end of seventh tergite almost to eighth tergite; eighth tergite ca. 2× as long as wide, longitudinally divided anteriorly for ca. 1/3 length of sclerite, with several tiny setae along posterior margin; ovipositor elongate-protrusible; cerci long, more than 3 times as long as high. Ninth segment to end of fused cerci 0.85 mm long and 3.5 times as long as length of sixth tergite (n=2).

Pupa. As for *C. connata* (Figs. 83–84) but without facial protuberances. Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, diverging only apically, acutely triangular in lateral view.

Larva. **Third instar**: Length, 2.9–3.3 mm (n=6). White to orange. Body widest near middle, tapering to ends, broader than thick, deeply sulcate between segments. Spatula (Fig. 143): shaft quadrate, its anterior end slightly concave between the broad but acute, widely separated anterior teeth, not extending appreciably laterad of teeth. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side on all segments; terminals 8; sternals 2 on thoracic, 4 on abdominal segments; laterals 3 per side, usually with long seta, occasionally one of the 3 without seta; ventrals 1 per side on thoracic and first through seventh abdominal segments, with setae, 2 per side on eighth abdominal segment, one or both with seta. Length of dorsals, pleural, and terminals approximately as long as width of spiracles, slightly shorter. **Second instar**: Length 1.2–1.4 mm (n=7). Spatula (Fig. 165): bell-shaped, widening posteriad of acute anterior tooth, the tooth less than 1/2 length of shaft. Integument evenly spinulose, ventral spinules more diminutive than those on dorsum and not appreciably larger on venter of thorax than on abdomen. Papillae: as for third instar except that 1 or 2 of the 3 laterals per side may have no seta. Dorsal, pleural, and terminal setae subequal in length, subequal to spiracular width.

Type material.—*Holotype*: female, sugarberry, Alexandria, Louisiana, X-29-2010, J. C. Moser, emerged III-9 to 25-2011, deposited in USNM.

Etymology.—The name *ramicola* means "growing on branches," the usual site for the galls of this species.

Affinities.—See under *C. semenrumicis* concerning the close similarity and presumed affinity among it, *C. ramicola* and *C. ovata*. Second and third instar larvae of these three species are indistinguishable.

Biological notes.—Galls of this species mostly appear late in the season. Although seen as early as May in Alexandria, Louisiana, they were much more common there from August through October. In late September, many still contained second instars but by October all contained third instars. This is the only gall we have seen that may persist on branches into the next spring, and then not with viable larvae but with dead larvae or parasitoids. This gall may appear similar to those of *C. aciculata*. Galls of the latter species are always on the leaves and their attachment to the leaf is only half the diameter of the gall. Galls of *C. ramicola* are usually on twigs and their attachment to the substrate is at least as wide as the gall. The larvae of the two species are distinct.

Gastrancistrus sp. was reared in spring from galls of *C. ramicola* collected the previous summer in Alexandria, Louisiana.

Distribution (Map 16).—This species is restricted to southeastern U.S. and has been found only on sugarberry: **Georgia**: Monroe Co. **Louisiana**: Alexandria, Pineville. **Mississippi**: Grenada, Greenville. **Tennessee**: Memphis. **Texas**: Donie, Holland, Lockhart, Lufkin, Marlin, 1.6 mi. E Sparks (Bell Co.).

Specimens of *C. ramicola* examined.—**Louisiana**: Alexandria, VII-16-2009, JCM, 3 second instars, 1 pupal exuviae, emerged IV-10-2010; Alexandria, VIII-7-2009, JCM, 1 second and 1 third instar; Alexandria, VI-20-2010, JCM, 2 second instars; Alexandria, VII-11-2010, JCM, 2 third instars; Alexandria, IX-5-2010, JCM, 2 second instars; Alexandria, IX-12-2010, JCM, 4 third instars; Alexandria, X-10-2010, JCM, 3 second and 3 third instars; Alexandria, X-29-2010, JCM, 3 ♂, 2 ♀ (including holotype), emerged III-9 to 25-2011; Pineville, IX-4-2008, JCM, 2 second instars; Pineville, V-24-2009, 1 second instar, JCM, 2 second instars. **Mississippi**: Greenville, IX-4-2008, RJG, 3 second instars. **Texas**: Lufkin, X-11-2008, JCM, 3 third instars.

Celticecis semenrumicis (Patton)

semenrumicis Patton 1897: 248 (*Cecidomyiaceltis*), with reference to gall #31 of Riley 1890: 613; Wells 1916: 275, Plate XVII, Figs. 15 (3 separate illus.; as *Cecidomyia* sp.); Felt 1918: 122 (*Cecidomyia*); Felt 1940: 233

(Fig. 190), as *Cecidomyia* sp.; Gagné 1983: 437 (*Celticecis*).

Description.—*Gall* (Figs. 36–38; Plate 1, Fig. 15). On twigs, occasionally on petioles or stronger veins on either side of the leaf; upright, with 3–6 prominent, longitudinal, narrow, lateral wings and long, slender, curled apex; surface naked, matte, green turning tan, or wholly or partly red; 6–8 mm long, 4–6 mm wide at mid-length; connection to twig or leaf a broad, persistent callus; when on leaf apparent on reverse as a widened vein; gall in cross section an elongate-ovoid larval chamber surrounded by thin wall beyond which the wings radiate.

Adult. Antenna with 17 flagellomeres in male (n=1) and 17–18 in female (n=2). Wing length: male, 2.5 mm (n=1); female, 2.5 mm (n=3). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with double row of posterior setae intermixed with scales that cover posterior 2/3 of sclerite; eighth tergite weakly sclerotized beyond anterior pair of trichoid sensilla, with single row of sparse posterior setae and no scales along posterior margin. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites with 1–2 rows of posterior setae except sixth with 2 rows, without lateral setae, and covered with scales; seventh tergite less than 1/2 width of sixth tergite, quadrate, slightly wider than long, with 2–3 rows of posterior setae, scales only posteriorly; uneven, pigmented area extending from posterior end of seventh tergite almost to eighth tergite; eighth tergite ca. 2× as long as wide, longitudinally divided anteriorly for ca. 1/3 length of sclerite, with several tiny setae along posterior margin; ovipositor elongate-protrusible; cerci long, more than 3 times as long as high. Ninth segment to end of fused cerci 0.85 mm long and 3.5 times as long as length of sixth tergite (n=2).

Pupa. As for *C. connata* (Figs. 83–84) but without facial protuberances. Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, diverging only apically, acutely triangular in lateral view.

Larva. **Third instar**: Length, 1.8–4.0 mm (n=10). Yellow. Body widest at middle, tapering to ends, broader than thick, moderately furrowed between segments. Spatula (Fig. 144): with two narrow, acute anterior teeth each almost 2× as long as basal width and separated from one another by distance subequal to their basal width; large shaft quadrate except concave anteriorly between the teeth. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals per side on all thoracic and abdominal segments; 8 terminals; 2 sternals on thoracic segments, 4 on first through eighth abdominal segments; 2 laterals per side usually with prominent setae nearly as long as setae on adjacent ventral papillae, but occasionally one on one side lacking seta; 1 ventral per side with seta except 4 on eighth abdominal segment, usually with setae, occasionally 1 or 2 without. Dorsal, pleural and terminal setae of medium length, ca. as long as width of spiracles. **Second instar**: Length, 1.2–2.1 mm (n=10). White to yellow. Spatula (Fig. 166): more or less triangular, acute anterior tooth less than 1/2 length of shaft; shaft widening from the base of tooth to broad posterior limit. Body evenly covered with spinules, those of venter not larger on thorax than elsewhere. Length of papillae relative to spiracles as for third instar.

Type material.—*Syntypes*: 14 galls on three stems and one leaf, the plant parts each on separate pins, each pin originally labeled only "104L." The number refers to information in an old Department of Agriculture card file that includes the following: "104L. June 25/74." The galls were collected one day later than the types of *oviformis*, so are presumably also from Columbia, Missouri. The host is northern hackberry, based on characters of the leaf.

Etymology.—Patton (1897) named this species *semenrumicis* based on Riley's (1890) remark that the galls bore a close resemblance to the winged seed capsule of a *Rumex* (dock).

Affinities.—*Celticecis semenrumicis*, *C. ramicola*, and *C. ovata* are distinguishable mainly from their galls. Galls of all three species are usually found attached to twigs. Those of *C. semenrumicis* ultimately develop distinct wings, are hairless, have a slender, curled apex, dehisce by early summer, and are known from the Mississippi Basin and Texas. Galls of *C. ramicola* have the same general distribution, are also hairless but never winged, have a short, straight apical extension, develop in late summer and early autumn and are slow to dehisce, in some cases persisting through late autumn. Galls of *C. ovata* are not sympatric with those of the other two, are instead more northern and eastern and hairy and wingless. Larvae of all

three species have generally similar-shaped spatulas in second and third instars and have setose lateral papillae and mostly setose eighth abdominal ventral papillae. Adults of *C. semenrumicis* and *C. ramicola* are similar to one another. In particular the female eighth tergite of both species is longitudinally divided anteriorly. Adults of *C. ovata* are unknown.

Biological notes.—Galls first grow to their full length and only then develop wings. In Louisiana galls were found as early as late April on only partly expanded leaves, already with second instars. By June 6 only third instars were present, and galls dehisced readily although a few galls with viable full-grown larvae were found as late as August.

Gastrancistrus sp. was reared in spring from galls of *C. semenrumicis* collected the previous summer.

Distribution (Map 17).—This species is known only from south-central U.S. on both northern hackberry and sugarberry. **Kansas**, northern hackberry: Lawrence. **Louisiana**, sugarberry: Alexandria, Pineville. **Missouri,** northern hackberry: Columbia. **Texas**, sugarberry: Bonham, Lockhart, Lufkin, San Antonio, Temple. Wells (1916) illustrated the anatomy of this gall based on work done while he was in Kansas and Ohio but did not state the provenance of his specimens.

Specimens of *C. semenrumicis* examined.—**Louisiana**, sugarberry: Pineville, V-24-2010, JCM, 3 second instars; Alexandria (all collected by JCM): III-29-2009, 3 second instars; V-15-2009, 3 second instars; V-6-2010, 1 third instar; V-13-2010, 1 third instar; V-30-2010, 1 second instar; VI-20-2010, 1 third instar and 3 ♀♀, emerged III-19-2011; VII-5-2010, 1 third instar; VII-18-2010, 1 third instar. **Missouri**, northern hackberry: Columbia, V-25-1874, C.V. Riley, 2 second instars. **Texas,** sugarberry: Bonham, VIII-7-1918, A.H. Hollinger, 1 third instar; Lockhart, J. Riemann, 1 ♂, emerged III-13-1957; Waters Dairy Rd., Temple, IV-28-2010, T.O. Robbins, 3 second instars.

Celticecis spiniformis (Patton)

spiniformis Patton 1897: 248 (*Cecidomyiaceltis*), with reference to gall #34 of Riley 1890: 614; Felt 1918: 123 (*Cecidomyia*); Felt 1940: 231 (*Cecidomyia*); Gagné 1983: 437 (*Celticecis*).

unguicula Beutenmüller 1907: 388, Plate XIII, Fig. 9 (galls) (*Cecidomyia*); Sears 1914: 384, Fig. 36 (gall) (*Cecidomyia*); Wells 1916: 269, missp. as *unguicola*, Plate XVII, Figs. 8, 8a–f (*Cecidomyia*); Felt 1918: 123 (*Cecidomyia*); Felt 1940: 234 (*Cecidomyia*); Gagné 1983: 437 (*Celticecis*). **New synonym**.

Description.—*Gall* (Figs. 2, 39–41; Plate 1, Figs. 8, 8a–f). On leaf lamina, usually on underside of leaf, often in groups; upright-conical; base flared, circular, flat to rounded; tapering evenly from base to sharply pointed apex; surface naked, glabrous, green, turning yellow to tan; 4–6 mm high and 3–4 mm wide at base; connection to leaf circular, flat, ca. 1/3 width of gall base; apparent on opposite side of leaf as slight, sometimes discolored convexity; gall in cross section of variable thickness beneath and around base of subcylindrical larval chamber, thinning abruptly between distal third and fourth, at which level gall apex breaks off upon adult emergence in spring.

Adult. Antenna with 14–16 flagellomeres in male (n=5) and 14–15 in female (n=5). Wing length: male, 2.4–2.6 mm (n=5); female, 2.3–2.6 mm (n=5). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with double row of posterior setae intermixed with scales that cover posterior 2/3 of sclerite; eighth tergite weakly sclerotized, with anterior pair of trichoid sensilla, single row of sparse posterior setae and no scales. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: (Figs. 69–70). First through sixth tergites with mostly single row of posterior setae except sixth with 2 rows, without lateral setae, and covered with scales; seventh tergite ca. 1/2 width of sixth tergite, quadrate, slightly wider than long, with 2–3 rows of posterior setae, scales covering posterior half; eighth tergite subequal to seventh, quadrate, slightly longer than wide, undivided longitudinally, with mostly double row of short setae along posterior margin and no scales elsewhere; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high. Ninth segment to end of fused cerci 0.49–0.52 mm long and 2.6–2.7 times as long as length of sixth tergite (n=5).

Pupa. (Figs. 91–92). Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, acutely triangular in lateral view. Face without protuberances.

Larva. **Third instar**: Length, 1.4–2.7 mm (n=9). Body elongate-ovoid, only slightly sulcate inter-

segmentally, anterior and posterior ends blunt except for pointed head. Spatula (Figs. 145–146): either with 2 anterior teeth and shaft generally trapezoid, narrowest at base and gradually widening laterad of the two anterior acute teeth, or with spatula similar to that of second instar with only one acute anterior tooth subtended laterally by anterior extensions of the shaft. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 4 terminals; 2 sternals on thoracic and first through seventh abdominal segments; 2 laterals per side of midline, setae if apparent shorter than socket diameter; 1 ventral per side on each thoracic and first through eighth abdominal segments, that of eighth abdominal segment lacking the seta. All papillar setae except those of laterals ca. as long as spiracular width. **Second instar**: Length 0.6–1.3 mm (n=8). Spatula (Fig. 167): with acute anterior tooth less than 1/2 as long as shaft, shaft much broader than tooth and with anteriorly directed extension on each side of tooth. Lateroventral spinules appreciably larger on thorax than on abdomen. Dorsal, pleural and terminal setae longer than spiracular width, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type material.—*Cecidomyiaceltis spiniformis* Patton: *Lectotype*: gall, **here designated**, from a series of 39 galls attached to two folded leaves on one pin, 107L, Columbus, Texas, VII-1879, deposited in the USNM. The type series was until recently labeled only as "107L." That code referred to data in a Department of Agriculture card file that provided the collection data. The host name was not included, but the leaf is definitely from a sugarberry. A second instar larva removed from the lectotype gall is mounted on a slide and labeled as extracted from the lectotype. All the galls in the type series are young galls that do not exhibit the expanded base of more mature galls. Second instars removed from several of them fit well the description of this species given here. Moser (1965: 10) designated "107L" as lectotype, but that number included all of the original syntypes, not just a single specimen, which a lectotype has to be (ICZN 1999). That designation is therefore invalid.

Cecidomyia unguicula Beutenmüller: *Lectotype*: **here designated**, female, recently mounted on a slide in Canada balsam, from syntype series originally consisting of two males and eight females from northern hackberry, Cincinnati, Ohio, R.S. Harvey (Beutenmüller 1907), deposited in AMNH. Only the eight females can be accounted for at present, seven in the AMNH and one in the Museum of Comparative Zoology in Cambridge, Massachusetts. Type galls are also represented in both museums. Some of the galls in the AMNH were opened to obtain larvae for comparison. The third instars we excised agree with the description given here for *C. spiniformis*. Wells (1916: 270) suggested that Beutenmüller's species might be the same as *C. spiniformis* Patton (as Riley's #34). Following a study of the type series and associated galls and larvae, we concur with Wells's opinion and consider *C. unguicula* a synonym of *C. spiniformis*.

Etymology.—The name *spiniformis* refers to the gall's spinelike shape; *unguicula* is Latin for "small fingernail" but the reference is unclear.

Remarks.—This is the only *Celticecis* species we know with two distinct kinds of spatula in the third instar. The spatula may have two anterior teeth (Fig. 145), as do third instars of almost all other *Celticecis* spp., or only a single tooth (Fig. 146) and otherwise resembling the second instar spatula. We call this second kind the "Ithaca type," because it was first reported by Moser (1965) in third instars of this species from Ithaca, New York. This peculiar spatula on the third instar, which we know to be the third instar because of the pebbled verrucae covering the entire body, is found in the more northern part of the species's range. It can be seen on specimens from Ithaca, New York, as well as from Pittsburgh, Pennsylvania; Union, Ohio; Lawrence, Kansas; Atkinson, Wisconsin; Hancock and Cabin John, Maryland; and Hedgesville, West Virginia. Both kinds of spatula were found in similar galls collected together in the last four sites listed. This "Ithaca type" spatula may occur even more commonly than we know because some of our other northern collections are represented here only by second instars or galls.

Affinities.—Nine species of *Celticecis* appear to form a natural group: *C. spiniformis*, *C. aciculata*, *C. acuminata*, *C. capsularis*, *C. conica*, *C. cupiformis*, *C. pilosa*, *C. subulata*, and *C. supina*. All form galls on the leaf lamina except for *C. supina* whose galls are attached to veins, usually minor ones. These species share a striking synapomorphy of the second instar on which the lateroventral spinules of the thorax are appreciably larger than elsewhere. These enlarged spicules are not always apparent

in second instars of *C. capsularis* or *C. cupiformis*, but specimens of both those species are tiny and have reduced dermal armature. These nine species share the loss of one pleural and one sternal papilla on each side of the first through seventh larval abdominal segments and of one ventral papilla on the eighth abdominal segment. Females share a moderately long ovipositor but with the quadrate eighth tergite not longitudinally divided and the fused cerci only ca. twice as long as high. Distinctions among these species lie in losses of additional larval papillae and differences in the shape of the spatula, as outlined in the key to larvae.

Biological notes.—Galls reach their ultimate length as a narrow cone (Fig. 41) before the base broadens to its full width, so young galls can at first be confused with those of *C. subulata*. The gall only later spreads out considerably at the base, which can be acute to well-rounded in cross section (Fig. 39). Wells (1916) gave a technical morphological description of the gall tissue accompanied by detailed histological drawings that are reproduced here (Plate 1). Second instars are white and third instars are initially white but the anterior segments eventually turn yellow. When full-grown, the larva spins a cocoon that extends only to the narrow part of the larval chamber where the tip of the gall will break off in spring. Galls were already evident in late March in central Louisiana on only partly expanded leaves and were first noticed already with second instars in early May in Maryland. At least some full-grown larvae had already formed cocoons in mid-June in Louisiana and late June in Maryland. Many galls still with second instars can be found through mid-July so growth appears staggered. Some galls with cocooned larvae may remain attached to the leaves into September in Maryland and into November in Louisiana where the leaves remain on the tree longer. This longer duration on the leaves is a habit shared by most of the nine species of the *C. spiniformis* group, unlike most galls of the remaining species that tend to dehisce as soon as the larvae have formed their cocoons.

Gastrancistrus sp. was reared in April, 2009 from galls of *C. spiniformis* collected the previous summer at both Falling Waters and Cherry Run, West Virginia.

Distribution (Map 18).—*Celticecis spiniformis* is a common, widespread species in the eastern half of the U.S., except in Florida where it is conspicuously absent. It is known from northern hackberry, sugarberry, dwarf hackberry and reticulated hackberry. Galls were collected from: **Arkansas**, sugarberry and northern hackberry: 4.4 mi. NW Emmet, Searcy. **Georgia**, sugarberry: Augusta; Lake Tobesofkee, Bibb. Co.; Musella; dwarf hackberry: Houston. Co, Monroe Co. **Illinois**, northern hackberry: Rock Island. **Iowa**, northern hackberry: Ackworth, Ames, Cedar Rapids, Lansing, Pisgah. **Kansas**, northern hackberry: Lawrence. **Kentucky**, northern hackberry: Georgetown, Lawrenceburg, Winchester. **Louisiana**, sugarberry: Alexandria, Pineville. **Maryland**, northern hackberry: Cabin John, Hancock, Williamsport. **Mississippi**, sugarberry: Greenville, Stoneville. **Missouri**, northern hackberry: Columbia. **New York,** northern hackberry: Ithaca. **Ohio**, northern hackberry: Ashville, Batavia, Cincinnati, Columbus, Sandusky (Sears 1914), Union. **Pennsylvania**, northern hackberry: McKees Half Falls, Pittsburgh. **South Dakota**, northern hackberry: Brookings. **Tennessee**, northern hackberry: Nashville. **Texas**, sugarberry: Austin, Belton (also on netleaf hackberry), College Station, Columbus, Donie, Holland, Lufkin, Luling, 1.6 mi. E Sparks (Bell Co.),Temple. **Vermont**, northern hackberry: Burlington. **Virginia**, northern hackberry and sugarberry, Suffolk. **West Virginia**, northern hackberry: Cherry Run, Falling Waters, 6 mi. NW Hedgesville, Paw Paw. **Wisconsin**, northern hackberry: Atkinson, Cross Plains.

Specimens of *C. spiniformis* examined (third instars with second instar spatulas are indicated as "Ithaca type").—**Arkansas**, sugarberry: 4.4 mi. NW Emmet, VIII-20-2009, T.O. Robbins, 1 third instar. **Georgia**, sugarberry: L. Tobesofkee, Bibb Co., VI-5-2011, J. & R. Payne, 2 second instars. **Iowa**, northern hackberry: Ackworth, Warren Co., VI-15-2011, J. Pearson, second instar; Ames, IX-27-2010, M.J. Hatfield, 1 third instar; Lansing, VIII-2010, M.J. Hatfield, 1 third instar. **Kansas**, northern hackberry: Lawrence, VIII-25-1983, RJG, 9 third instars, 3 of "Ithaca type"; VI-5-2009, G.-S. Tung, 3 second instars. K**entucky**, northern hackberry: Lawrenceburg, IX-1-2008, RJG, 3 third instars; Georgetown, VI-23-2010, RJG, 1 second instar. **Louisiana**, sugarberry: Alexandria, VIII-7-2009, JCM & RJG, 3 third instars; Alexandria, VI-20-2010, JCM, 1 third instar; IX-5-2010, JCM, 5 third instars. **Maryland**, northern hackberry: Cabin John, V-12, 2009, RJG, 1 second instar; Cabin John, VIII-16- 2009, RJG, 1 third instar, "Ithaca type"; Cabin John, VII-5-2010, RJG,

2 third instars, "Ithaca type", 3 ♂, 3 ♀, pupa, emerged III-15 to 24-2011; Cabin John, VII-22-2010, RJG, 2 third instars; Cabin John, V-20-2009, RJG, 3 second and 2 third instars; Hancock, VI-22-2010, RJG, 7 third instars, 3 of "Ithaca type"; Glen Echo, VIII-7-2008, RJG, 2 third instars, "Ithaca type". **Mississippi**, sugarberry: Stoneville, IX-5-2008, RJG, 3 third instars, 7 ♂, 8 ♀, 2 pupae, emerged IV-2009. **Missouri**, northern hackberry: Columbia, VI-24-1874, C.V. Riley, 3 second instars. **Ohio**, northern hackberry: Ashville, VII-20-2011, RJG, 2 third instars; Batavia, VII-20-2011, RJG, third instar; Cincinnati, undated, R.S. Harvey, lectotype ♀ and 7 ♀ paralectotypes of *Cecidomyia unguicula*, also 3 third instars excised from topotype galls; Union, VI-22-2010, RJG, 2 third instars, "Ithaca type". **New York**, northern hackberry: Ithaca, VI-9 to VII-17-1957, JCM, 13 second and 7 third instars, "Ithaca type". **Pennsylvania**, northern hackberry: Pittsburgh, VI-28-2011, P. Woods, 2 third instars, "Ithaca type". **Texas**, sugarberry: College Station, VI-4-2009, RJG, 3 third instars; Columbus, VII-1879, C.V. Riley, 3 second instars ex lectotype and 2 paralectotypes of *Cecidomyiaceltis spiniformis*; Kurth Lake, near Lufkin, X-9-2008, JCM, 2 third instars. **Vermont**, northern hackberry: Burlington, VI-28-2011, C. Eiseman, 4 second instars. **West Virginia**, northern hackberry: Cherry Run, VIII-28-2010, RJG, 1 third instar, 1 ♂, 1 ♀, pupa, emerged IV-10-2011; 6 mi NW Hedgesville, VIII-9-2008, RJG, 4 third instars, two of "Ithaca type"; 6 mi NW Hedgesville, IX-13-2008, RJG, 1 third instar, 3 ♀, emerged IV-2009; 6 mi NW Hedgesville, IX-12-2009, RJG, 2 ♀ emerged IV-12-2010. **Wisconsin**, northern hackberry: Fort Atkinson, VIII-17-1923, 6 third instars, one of "Ithaca type".

Celticecis subulata Gagné, new species

Description.—*Gall* (Figs. 2, 42–43). On leaf lamina, usually on underside of leaf, single or in groups; upright, elongate-conical, tapering evenly from sharply angled base to pointed apex; surface glabrous, green, turning tan to brown; 6–9 mm high and 2–3 mm wide at base; connection to leaf circular, flat, ca. 1/2 width of gall base, apparent on opposite side of leaf as slight discoloration, rarely as small convexity; gall in cross section thin-walled especially beyond 2/3 height, the cylindrical larval chamber extending from base of gall to apex.

Adult. Antenna with 13–15 flagellomeres in male (n=4) and 15–16 in female (n=5). Wing length: male, 2.2–2.4 mm (n=4); female, 2.1–2.2 mm (n=5). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with double row of posterior setae intermixed with scales that cover posterior 2/3 of sclerite; eighth tergite weakly sclerotized, with single row of sparse posterior setae and no scales. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites with mostly single row of posterior setae except sixth with 2 rows, without lateral setae, and covered with scales; seventh tergite ca. 1/2 width of sixth tergite, quadrate, slightly wider than long, with 2–3 rows of posterior setae, scales covering posterior 2/3 of sclerite; eighth tergite quadrate, slightly longer than seventh but narrower, undivided longitudinally, with mostly two rows of short setae along posterior margin; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high. Ninth segment to end of fused cerci 0.45–0.50 mm long and 2.4–2.5 times as long as length of sixth tergite (n=3).

Pupa. As for *C. spiniformis* (Figs. 91–92). Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, acutely triangular in lateral view. Face without protuberances.

Larva. **Third instar**: Length, 1.4–2.7 mm 9 (n=10). Body elongate-ovoid, only slightly sulcate intersegmentally, anterior and posterior ends blunt except for the pointed head. Spatula (Fig. 148): shaft generally trapezoid, narrowest at base and flaring laterad of the two anterior acute teeth. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 4 terminals; 2 sternals on thoracic and first through seventh abdominal segments; 2 laterals on each side of midline, their setae if apparent shorter than socket diameter; 1 ventral per side on each segment of thoracic and first through eighth abdominal segments, that of eighth abdominal segment lacking a seta. All papillar setae except those of the shorter laterals ca. as long as spiracular width. **Second instar**: Length 0.9–1.3 mm (n=5). Spatula (Fig. 168): with large, acute anterior tooth more than 1/2 as long as shaft, the shaft cruciate, much broader than tooth. Lateroventral spinules appreciably larger on thorax

than on abdomen. Dorsal, pleural and terminal setae longer than spiracular width, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type material.—*Holotype*: third instar larva, from gall on sugarberry, Kurth Lake, near Lufkin, Texas, X-9-2008, J.C. Moser, deposited in USNM.

Etymology.—The name *subulata* means "awl-shaped," with reference to the shape of the gall.

Affinities.—The larva of this species has the same papillar pattern as that of *C. spiniformis*. The two species differ in the shape of their spatula, the third instar of *C. subulata* with more narrowly acute apical teeth and the second instar with a much more robust tooth and shaft, the latter without the anterior projections of the shaft on each side of the tooth as seen in *C. spiniformis*. The second instar spatula of this species and that of *C. pilosa* are both extremely large, unlike *C. spiniformis*, and generally resemble one another except that the tooth of *C. subulata* is much larger than that of *C. pilosa*. See under *C. spiniformis* for additional discussion.

Biological notes.—In central Louisiana, young galls can be found already with second instars in late March on partly expanded leaves. Full-grown, cocooned larvae as well as some larvae still in the second instar were found in galls in late May. Galls may remain on the leaves through the season and dehisce in September and October. Cocoons extend from the bottom of the larval chamber to about 2/3 height at which point the gall will easily divide the following spring. Larvae are white until later in the third instar when their anterior half turns yellow.

Gastrancistrus sp. was reared in spring from galls of *C. subulata* collected the previous summer in Alexandria, Louisiana and Temple, Texas.

Distribution (Map 19).—This southern U.S. species is found from Georgia and Florida west to Arkansas and Texas. Galls were collected from sugarberry, dwarf hackberry and netleaf hackberry. **Arkansas**, sugarberry: 4.4 mi. NW Emmet. **Florida**, sugarberry: Edgewater, Gainesville, Mims, Williston. **Georgia**, dwarf hackberry: Monroe Co. **Louisiana**, sugarberry: Alexandria, Pineville. **Mississippi**, sugarberry: Greenville, Stoneville. **Texas**, sugarberry: Belton (also on netleaf hackberry), Bertram, College Station, Donie, Holland, Lufkin, Luling, Nacogdoches, Temple.

Specimens of *C. subulata* examined (all from sugarberry unless otherwise noted).—**Florida**: Edgewater, VI-26-2009, K.L. Hibbard, 5 third instars; Mims, V-27-2010, RJG, 3 second instars; Mims, V-29-2010, K.L. Hibbard, 6 third instars; Williston, IV-24-2009, K.L. Hibbard, 4 second instars; Williston, V-7-2009, K.L. Hibbard, 4 second instars. **Louisiana**: Alexandria, IX-21-2008, JCM, 2 third instars; Alexandria, VIII-7-2009, JCM & RJG, 4 third instars; Alexandria, V-30-2010, JCM, 3 second instars; Alexandria, VII-11-2010, JCM, 4 ♂, 5 ♂, 3 pupae emerged III-26-2011; Alexandria, VII- 24-2010, JCM, 2 third instars; Pineville, IX-4-2008, JCM, 2 third instars. **Mississippi**: Greenville, IX-4-2008, RJG, 3 third instars; Stoneville, IX-5-2008, RJG, 3 third instars. **Texas**: Belton (also on netleaf hackberry), VIII-4-2009, T.O. Robbins, 3 third instars; College Station, VI-4-2009, R. Billings, 2 second instars; Lufkin, X-9-2008, JCM, 2 third instars; Temple, VIII-4-2009, T.O. Robbins & RJG, 1 ♀ emerged IV-9-2010; Temple, Waters Dairy Rd, IV-27-2010, T.O. Robbins, 2 second instars.

Celticecis supina Gagné, new species

Cecidomyia sp., Wells 1916: 273, Plate XVII, Figs. 11, 11a.

Description.—*Gall* (Figs. 44–46; Plate 1, Figs. 11, 11a). Reclinate along major or minor veins, almost always on lower leaf surface; subcylindrical, tapering gradually or just before apex; surface striate to rugose, green at first, turning yellow to tan, usually with sparse white hair not obscuring gall surface; 3–4 mm long, 1–2 mm wide near base; wall thin, larval chamber shaped as for gall; gall on opposite side of leaf apparent as a slight discolored convexity.

Adult. Antenna with 13 flagellomeres in male (n=1) and 11–12 in female (n=5), female flagellomeres reduced in size and number of setae as for *C. cupiformis*. Wing length: male, 1.5 mm (n=1); female, 1.3–1.5 mm (n=5). **Male abdomen**: First through sixth tergites with mostly single row of posterior setae, without lateral setae, and covered with scales; seventh tergite rectangular, with single sparse row of posterior setae and no scales anteriad of setae; eighth tergite weakly sclerotized, without posterior setae and no scales. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through sixth tergites with single row of posterior setae, without lateral setae, and covered with scales; seventh tergite ca. ½ width of sixth tergite, quadrate, slightly wider than long, with

single row of posterior setae, without scales anteriad of posterior setae; eighth tergite quadrate, subequal to seventh, undivided longitudinally, with sparse, short setae along posterior margin; ovipositor elongate-protrusible; cerci cylindrical, ca. 2× as long as high. Ninth segment to end of fused cerci 0.34–0.35 mm long and 3.4–3.5 times as long as length of sixth tergite (n=5).

Pupa (Figs. 93–94). Antennal bases bilaterally compressed, keel-like ventrally, closely adjacent, acutely triangular in lateral view. Face without protuberances.

Larva. **Third instar**: Length, 1.2–1.8 mm (n=8). White. Body cylindrical, blunt at ends, the segments only slightly sulcate. Spatula (Fig. 147): with short shaft, slightly wider than long, extending laterad of acute anterior teeth, the teeth ca. 2/3 length of shaft, their bases nearly touching. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 4 terminals; 2 sternals on both thoracic and abdominal segments; 2 laterals per side, their setae if apparent shorter than socket diameter; 1 ventral per side on each segment of thoracic and first through eighth abdominal segments, that of eighth abdominal lacking the seta. Dorsal, pleural, and terminal setae approximately as long as spiracular width or slightly shorter, the ventrals slightly shorter than the dorsals. **Second instar**: Length 0.6–1.0 mm (n=6). Spatula (Fig. 169): with apically obtuse to acute tooth and large, broad shaft at least 3 times width of tooth. Lateroventral spinules appreciably larger on thorax than on abdomen. Dorsal, pleural and terminal setae longer than spiracular width, dorsals and pleurals of eighth abdominal segment and terminals subequal in length.

Type material.—*Holotype*: third instar larva, sugarberry, Alexandria, Louisiana, VI-21-2009, J.C. Moser, deposited in USNM.

Etymology.—The name *supina* refers to the reclinate position of the gall on the leaf.

Affinities.—The tiny galls of this species produce small adults that are among the smaller ones in *Celticecis*. See under *C. spiniformis* for further discussion.

Biological notes.—This early-developing gall was evident in early May in Louisiana and by mid-May in Maryland, in both places already with second instars. In Louisiana galls found with third instars by May 23 in which some had cocooned by June 13. Cocoons fill the larval cavity except for the narrower apex that breaks off when adult emerges in spring.

Several parasitoids were reared in spring from galls of *C. supina* collected the previous summer. These were: two species of *Gastrancistrus* sp. and *Trichacis pyramidalis* Masner from Cabin John, Maryland; *Trichacis bison* Masner from Cabin John, Maryland and Alexandria, Louisiana; and *Trichacis* sp. near *celticola* Masner and *Trichacis* sp. near *cornicola* Masner from Alexandria, Louisiana.

Distribution (Map 20).—This species is generally widespread in eastern U.S. except that it appears to be absent in the southeast. It is found on northern hackberry, sugarberry and netleaf hackberry. Galls of *C. supina* were collected from: **Iowa**, northern hackberry: Ames, Cedar Rapids. **Kansas**, northern hackberry: Lawrence. **Kentucky**, northern hackberry: Georgetown, Lawrenceburg, Winchester. **Louisiana**, sugarberry: Alexandria, Pineville. **Maryland**, northern hackberry: Cabin John, Glen Echo, Hancock. **Missouri**: northern hackberry, Columbia. **Ohio**, northern hackberry: Batavia, Columbus, Sandusky. **Tennessee**, northern hackberry: Nashville. **Texas**, sugarberry: Bertram, Belton, Georgetown, Marlin. **West Virginia**, northern hackberry: Cherry Run, Falling Waters, Paw Paw.

Specimens of *C. supina* examined: **Kentucky**, northern hackberry: Lawrenceburg, IX-1-2008, RJG, 3 third instars, 1 ♀, emerged IV-19-2009; Winchester, VI-23-2010, RJG, 3 second instars. **Louisiana**, sugarberry: Alexandria, V-16-2010, JCM, 3 third instars; Alexandria, V-30-2010, JCM, 2 third instars; Alexandria, VII-5-2010, JCM, 1 ♂, 3 ♀, pupa, emerged III-18-2011; Pineville, VI-24-2009, JCM, 3 third instars. **Maryland**, northern hackberry: Cabin John, VIII-7-2008, RJG, 3 third instars; Cabin John, VI-3-2009, RJG, 5 second instars; Cabin John, VIII-16-2009, RJG, 3 third instars, 3 ♀, pupa, emerged IV-2–5-2010; Glen Echo, VIII-7-2008, RJG, 1 third instar. **Texas**, sugarberry: Marlin, VIII-21-2009, T.O. Robbins, 4 third instars. **West Virginia**, northern hackberry: Falling Waters, VII-21-2009, RJG, 3 third instars.

Celticecis wellsi (Wells)

Phytophaga wellsi Wells 1916: 273, Plate XVII, Figs. 10 (gall), 10a (cross-section), inadvertently antedated in May the formal description of the species by Felt (1916) that appeared in September; Gagné 2004: 102 (*Celticecis*).

Phytophaga wellsi Felt 1916: 190; Felt 1918: 123 (*Phytophaga*); Felt 1940: 231 (*Phytophaga*); Gagné 1983: 437 (*Celticecis*); Gagné 2004: 102, as junior synonym of *C. wellsi* Wells.

Description.—*Gall* (Figs. 47–48; Plate 1, Figs. 10, 10a). On underside of leaf, in vein fork, usually perpendicular to leaf, often single but may occur in twos and threes; turbinate, widest beyond midlength, the apex flattened with diminutive apical tubercle in center; surface green turning brown, covered with variable but usually thick, abundant white pubescence; ca. 4 mm long, almost as wide as long; apparent on opposite side of leaf as slight, sometimes discolored convexity; in cross section, walls thickest on distal half, yellowish, woody, thinnest at center apex; larval chamber elongate-ovoid, as long as gall.

Adult. Antenna with 16 flagellomeres in male (n=1) and female (n=1). Wing length: male, 2.7 mm (n=1); female, 2.2 mm (n=1). **Male abdomen**: First through sixth tergites rectangular, with mostly single row of posterior setae, without lateral setae, elsewhere covered with scales; seventh tergite rectangular, with double row of posterior setae intermixed with scales that extend in coverage only slightly anterior to setal row; eighth tergite weakly sclerotized, without vestiture except for anterior pair of trichoid sensilla. Terminalia as for *C. celtiphyllia* (Figs. 119–120). **Female abdomen**: First through fifth tergites as for male; sixth tergite rectangular, ca. 2 ½ times as wide as long, with 2 rows of posterior setae and elsewhere covered evenly with scales; seventh tergite ca. 1/2 width of sixth tergite, quadrate, slightly wider than long, with 2–3 rows of posterior setae and scattered scales on posterior half; eighth tergite quadrate, as long as previous tergite but 1/2 as wide, undivided longitudinally, with 2 rows of short setae along posterior margin; ovipositor elongate-protrusible; cerci short, spheroidal, as long as high. Ninth segment to end of fused cerci 0.62 mm long and 3.2 times as long as length of sixth tergite (n=1).

Pupa. Unknown.

Larva. **Third instar**: Length, 2.6–3.1 mm (n=4). Yellow. Spatula **(**Fig. 149): shaft generally ovoid, the two acute anterior teeth separated from one another by ca. 1/2 their basal width. Papillae: 6 dorsals, except 2 on eighth abdominal segment; 2 pleurals on each side of thoracic and eighth abdominal segments, 1 on each side of first through seventh abdominal segments; 6, 7, or 8 terminals; 2 sternals on thoracic, 4 on abdominal segments; 2 laterals per side, their setae long; 1 ventral per side on each segment of thoracic and first through eighth abdominal segments, that of eighth abdominal lacking the seta. Dorsal, pleural, and terminal setae only ca. 2/3 length of spiracular width. **Second instar**: Length, 0.9–1.2 mm (n=7). Yellow. Spatula (Fig. 170): with acute, anterior tooth less than ½ as long and wide as ovoid shaft. Ventral spinules more diminutive than those on dorsum and not appreciably larger on thorax than on abdomen. Papillae as for third instar. Setae not longer than width of spiracles.

Type material.—*Phytophaga wellsi* Wells: *Lectotype*: **here designated**, gall described in Wells 1916 on p. 273 and illustrated on Plate XVII, Figs. 10–10a (Plate 1, this paper), "collected presumably in the vicinity of Columbus, O[hio]" (teste Felt 1916: 190).

Phytophaga wellsi Felt: *Lectotype*: **here designated**, female, a2713, "collected presumably in the vicinity of Columbus, O[hio]", NYSM. Paralectotypes, male, larvae, same data as lectotype.

Etymology.—The name *wellsi* was evidently coined by Felt to honor the collector, B.W. Wells.

Remarks.—Wells (1916) wrote that the gall was covered with short pubescence, but the specimens we have are more or less completely covered with long hairs, some crinkly. We suspect that Wells's specimen lost the hair through handling. In fact, Wells did not always note or draw hairs or draw them to their fullest extent. As examples, he did not draw hairs on galls of *C. supina* (Plate 1, Fig. 11) although that gall usually has hairs, and he drew what looks like very short pubescence for galls of *C. celtiphyllia* (Plate 2, fig. 9) when in fact they are usually covered with longer hairs. Felt (1916) wrote that the galls of *C. wellsi* were sparsely clothed with a whitish, appressed pubescence. This description agrees better with the galls we have seen.

Affinities.—See discussion under *C. pubescens*.

Distribution (Map 21).—This species is known from the midwestern U.S. and Georgia, on northern hackberry and sugarberry: **Georgia**, sugarberry: Monroe Co.; **Illinois**, northern hackberry: Peoria; **Iowa**, northern hackberry: Ames, Cedar Rapids; **Kansas**, northern hackberry: Manhattan; **Kentucky**, northern hackberry: Lawrenceburg; **Ohio**, northern hackberry: Ashville, Columbus. An illustration of a gall from Florida in Hodges

et al. (2006) identified as that of *C. wellsi* shows instead the gall of a psyllid.

Specimens of *C. wellsi* examined (all on northern hackberry).—**Georgia**: Monroe Co., V-1-2011, J. & R. Payne, 2 second instars; **Iowa**: Ames, IX-27-2010, M.J. Hatfield, 3 third instars; **Kentucky**: Lawrenceburg, IX-1-2008, RJG, 2 third instars; **Ohio**:Ashville, VII-20-2011, RJG, 3 second and 3 third instars; vic. Columbus, syntype series *C. wellsi* Felt: 1 third instar without collection date, 1 ♂ and 1 ♀, emerged III-20-1916.

GENUS *PERACECIS* GAGNÉ, NEW GENUS

Type-species, *Peracecis fugitiva* Gagné, by present designation.

Diagnosis.—This monotypic genus belongs to the cecidomyiine supertribe Lasiopteridi based on the following combination of characters: the irregular number of antennal flagellomeres, the single node and simple circumfila of the male flagellomeres, the lack of a dorsal occipital protuberance, the presence of gonocoxal lobes sheathing the aedeagus and of setae on the ventral papillae of the larval eighth abdominal segment. *Peracecis* is one of the few lasiopterid genera with no break near the juncture of wing veins C and R_5. The genus is unique among Cecidomyiinae for the variation in shape of the male hypoproct from entire to deeply incised (Figs. 175–177) and for the unstable nature of the tarsal claws that have teeth that may originate from any part of the ventral surface of the claw and that may be once or twice divided (Figs. 173–174). The adult stage is otherwise superficially similar to *Celticecis*, particularly in having an undivided gonocoxal lobe sheathing one side of the aedeagus and the lack of a separation in the costal wing vein at its juncture with R_5. Both characters are rare among Lasiopteridi. The larval stage of *Peracecis* is quite different from that of *Celticecis*, preserving the entire complement of papillae, particularly all four triplets of the lateral papillae, and the long shaft of the spatula. The larva has a bilobed terminal segment, another unusual feature for Lasiopteridi.

Description.—*Adult*. **Head**: Eyes large, connate, facets circular, closely approximate on ventral, bulging part of eyes and dorsally, but more widely separated opposite insertion of antennae. Occiput without dorsal protuberance. Frons with 3–8 setae and 0 scales (n=10). Clypeus without setae or scales. Labrum without external scales. Labellum separate, hemispherical with several setae laterally. Palpus 4segmented, the segments not always fully separate, with many short and long setae and scales. Antenna (Fig. 99): scape subcylindrical, with several setae laterally and many scales ventromesally; pedicel short-spheroid, covered with setae on ventral half and with a single horizontal row of setae dorsally; male flagellomeres with node and distinct, bare necks, except the short-pyriform ultimate flagellomere; nodes with two simple horizontal circumfila on ventral half that may or may not connect laterally before evanescing on dorsum, with mostly single row of short setae basad of proximal circumfilum, stronger, basally recurved setae covering venter of node between circumfila but many fewer dorsally, and several long, straight setae just basad of distal circumfilum on venter, the entire node otherwise covered with setulae; female flagellomeres (Figs. 171–172) noticeably decreasing in size along length of antenna, all pyriform and without necks, ventrally with variable horizontal circumfila that may continue separately dorsally or fuse, with one or more vertical connectives, a mostly single horizontal row of straight setae extending around node basad of proximal circumfilum, fewer dorsally than ventrally, and a single row of longer, basally recurved setae between the two circumfila on venter but absent dorsally, the node otherwise covered with setulae. **Thorax**: Scutum with 4 longitudinal rows of setae mixed with scales. Scutellum with lateral group of setae mixed with scales on each side. Anepimeron covered with scales on dorsal half, bare ventrally, anepisternum covered with setae and scales, pleura otherwise bare. Wing: R_5 thick, nearly straight, joining C before wing apex, C not broken at juncture with R_5, Rs not apparent, M_3 weak, Cu forked. Legs thickly covered with scales; tarsal claws (Figs. 173–174) rounded beyond mid-length, simple or toothed, the teeth if present not necessarily basal and may be divided once or twice apically; empodia as long as claws; pulvilli ca. ½ length of claws. **Male abdomen**: First through seventh tergites rectangular, each with pair of anterior trichoid sensilla, a single to mostly double row of posterior setae except for a short lacuna medially, without lateral setae, and elsewhere with uniformly spaced scales; eighth tergite sclerotized only on anterior 1/3, the remainder membranous, the only vesti-

ture the anterior pair of trichoid sensilla. Second through sixth sternites rectangular, with anterior pair of closely approximated trichoid sensilla, a mostly single row of setae along posterior margin, a single to double row of setae near mid-length anterior to a weakly sclerotized horizontal area of the sternite, and elsewhere with a uniform covering of scales; seventh sternite generally similar except for double row of setae posteriorly and sparse setae elsewhere; eighth sternite triangular, widest at the posterior margin, with pair of closely approximated anterior trichoid sensilla, a double row of posterior setae and covered on remainder of sclerite with mostly short seta-like scales. Terminalia (Fig. 100): cerci ovoid, with several apical and subapical setae; hypoproct (Figs. 175–177) entire to deeply incised, with usually 3 long setae on each apicolateral corner or lobe, evenly setulose dorsally and ventrally; gonocoxite laterally elongate-cylindrical, medial lobe subtending one side of aedeagus undivided, covered with setulae, apically with group of short setae on raised bases; gonostylus tapering from broad base to apex, setulose on dorsal half and most of venter, ridged beyond, evenly setose; aedeagus tapered to rounded apex; apodeme keel-like. **Female abdomen**: second to sixth tergite as for male except posterior setae more numerous with a double to triple row narrowing to single row medially; seventh tergite quadrate, unevenly pigmented, less so laterally at mid-length than elsewhere, with scale covering much sparser, absent laterally; eighth tergite as long and nearly as wide as seventh tergite, entire but with two separate longitudinal bars more darkly pigmented than elsewhere but not forming distinctly separate sclerites, with pair of trichoid sensilla anteriorly and several short setae along posterior margin. Second through sixth sternites as for male; seventh sternite with pair of anterior trichoid sensilla, 3 rows of posterior setae, no horizontal row of setae at mid-length, and scales only on posterior half; eighth sternite not differentiated. Ovipositor (Fig. 101) elongate-protrusible: extended eighth segment and entire ninth with scattered short setae along length, the ninth with two narrow, elongate lateral sclerites; fused cerci (Fig. 102) elongate cylindrical, covered with long, pointed setae, intermixed apically and subapically with shorter, blunt-tipped setae.

Pupa (Figs. 103–104). Integument unpigmented except at anterior angle of antennal base. Vertex convex, anterolaterally on each side with long seta situated on conspicuous convexity. Antennal bases obtusely angled ventroapically. Face convex, without projections; with more or less conspicuous triplet of papillae near base of each palpus, one of them setose. Frons with 2 short-setose papillae on each side of frons. Prothoracic spiracles elongate, gradually tapered to apex. Abdominal tergites, pleura and sterna evenly spiculose, the spicules slightly longer and closer together on tergites than elsewhere; tergites with horizontal row of 6 setose papillae.

Larva. **Third instar** (Figs. 105–106). Body spindle-form. Head directed anteriorly, apodemes slightly longer than head capsule. Antenna less than 2× as long as wide. Integument covered entirely with rounded verrucae except slightly pointed anteriomedially on venter of first through seventh abdominal segments. Spiracles present on first thoracic and first through eighth abdominal segments. Spatula (Fig. 178): with pair of acutely pointed anterior teeth at end of long shaft. Full complement of papillae present and setae present as in Fig. 19 of Gagné (1989) except ventral papillae of prothorax with short seta, only as long as width of papilla. Other ventral and the dorsal, pleural and terminal papillae ca. 1½ times as long as spiracle width. Terminal segment ending in two lobes each bearing 4 papillae.

Etymology.—*Peracecis* is of Greek derivation, from *pera* for pouch and *cecis* for gall, with reference to the leaf pouch gall made by the sole included species. The name is feminine.

Affinities.—As mentioned in the diagnosis, *Peracecis* and *Celticecis* share an undivided gonocoxal lobe sheathing the aedeagus and a solid lateral sclerite on each side of the female ninth abdominal segment. The costal wing vein is not separated at its juncture with R_5 in either genus. The larvae, however, are distinct, reflecting their different habits. *Peracecis fugitiva* forms simple pouch galls from which the full-grown larvae escape while *Celticecis* species cause complex, deciduous galls in which the larvae eventually pupate. Adults of the two genera are readily separated by the presence of teeth on most of the tarsal claws of *Peracecis* and their absence on tarsal claws of *Celticecis*. One other key difference is that the male hypoproct of *Peracecis* has, when divided into two lobes, several apical and subapical setae that are appreciably longer than the width of the lobe on which they are situated, whereas similar lobes of

Celticecis have but two or three setae that are no longer than the width of the lobes.

Peracecis shares with *Gliaspilota* Gagné (2008) the unusual dissimilar tarsal claws that may or may not have teeth regardless of the leg they are on. This convergence is presumably only coincidental because the tarsal teeth of *Peracecis* are unique among Cecidomyiinae in that they sometimes emerge from the middle of the claws and may even be once or twice subdivided. Any particular affinity between adults of the two genera beyond the dimorphic tarsal claws are not otherwise apparent.

Peracecis fugitiva Gagné, new species

Description.—*Gall* (Figs. 51–54). On leaf, an integral spherical blister usually of the leaf underside, and a narrow chimney on the opposite surface through which the full grown larvae eventually exit; green, the same color as the leaf, matte, with short white pile on the blister side, bare on the other; blister 4–7 mm in diameter, 3–4 mm high, the chimney on opposite side of leaf ca. 2 mm long; gall thin-walled, no thicker than normal leaf tissue.

Adult. Antenna with 16–18 flagellomeres in male (n=10) and 17–18 in female (n=10). **Thorax**: Wing: length, 2.5–2.7 mm in male (n=5), 2.7–3.0 mm in female (n=10). **Male abdomen**: Terminalia as in Fig. 100, 175–177). **Female abdomen**: Ovipositor as in Figs. 101–102; ninth segment to end of fused cerci 0.80–0.85 mm long and 2.8–2.9 times as long as length of sixth tergite (n=5).

Pupa. As in Figs. 102–103.

Larva. **Third instar** (Figs. 105–106, 178): Length, 3.5-5.5 mm (n=10).

Type material.—*Holotype*: female, Alexandria, Louisiana, emerged III-12-2011 from larva collected IV-25-2010 on sugarberry, J.C. Moser, deposited in USNM.

Etymology. —The name *fugitiva* means "fugitive," with reference to the larval habit of leaving the gall when full grown.

Remarks.—Tavares (1925) described as "*Cecidomyia* sp." a blister leaf gall from *Celtis* sp. found in 1911 in Nova Friburgo, Rio de Janeiro. The description with no figures suggests a similarity to the gall of *P. fugitiva*. See under "Gall midges on *Celtis* reported outside North America" below for further details about the gall itself.

Biological notes.—Galls appear early in spring and were first noticed on April 16 in Alexandria, Louisiana and on April 7 in Holland, Texas when the larvae were already in their third instar. On May 3 to 9 in Alexandria larvae appeared full-grown, and by May 19 most had dropped to the soil. In Bibb County, Georgia a few larvae were recovered from galls collected on June 3. Galls are integral to the leaves so their shrivelled remains can be found throughout the season where they occur. Third instars are white, spindle-form and very active. As many as 15 larvae may be found in one gall. *Peracecis* larvae were observed crawling out of the galls through the chimney on the upper leaf surface. From galls artificially cut open, larvae simply wriggled out and dropped to the substrate provided. The larvae immediately burrowed into the damp peat moss. Inquilinous *Parallelodiplosis acernea* larvae were a common inhabitant in galls from Alexandria, Louisiana. They were red, also very active, and burrowed into the substrate along with *P. fugitiva*. By July larvae of *P. fugitiva* in the peat moss were found to have spun cocoons. Cocoons still contained larvae in early February when the pots were removed from the refrigerator.

All adult rearings of this species were from galls collected in Alexandria, Louisiana from IV-19–25- 2010. Adults of both sexes began to emerge on March 9 and continued to do so daily until March 27 for a total of 59. One *P. acernea* emerged on each of four occasions between March 19 and March 27, and then several each day from March 28 until April 7 for a total of 31. The delay between the emergence of *P. fugitiva* from March 9–27 and *P. acernea* between March 19 and April 7 might serve to give the *Peracecis* time to lay its eggs before the *Parallelodiplosis* lays its own eggs in their proximity before gall initiation.

A hymenopterous parasitoid preceded and another one followed emergence of *P. fugitiva* from the soil in spring of 2011. *Trichacis* sp. near *celticola* Masner was first to emerge with 24 specimens appearing between February 28 and March 7. *Peracecis fugitiva* emerged between March 9–27, during and following which, between March 20 and April 2, 11 specimens of a very tiny *Leptacis* sp. (Hymenoptera: Platygastridae) appeared. *Trichacis* sp. near *celticola* was reared also from *C. connata* and *C. supina* but the *Leptacis* sp. was reared during this study from only *P. fugitiva*.

Distribution (Map 22).—This mainly southern species does not appear to distinguish among hackberries. Fresh or spent galls were found in: **Georgia**, sugarberry: Bibb Co.; dwarf hackberry:

Houston Co. **Kansas,** northern hackberry: Lawrence. **Louisiana**, sugarberry: Alexandria, Pineville. **Texas**, sugarberry: Bertram, Belton, Burnet, Donie, Georgetown and Temple.

Specimens of *Peracecis fugitiva* examined.—**Georgia**: Bibb Co., VI-3-2011, J.&R. Payne, 2 third instars. **Louisiana**: Alexandria, IV-19-2009, JCM, 2 third instars; IV-19–25-2010, JCM, 7 third instars and 10 ♂, 10 ♀ and 5 pupae, emerged III-11–27-2011. **Texas**: Temple, Waters Dairy Road, IV-28-2010, T.O. Robbins, 5 third instars.

GENUS *PARALLELODIPLOSIS* RÜBSAAMEN

Parallelodiplosis Rübsaamen 1910: 297. Type-species, *Diplosis galliperda* Löw, monotypy; Gagné 2010: 321 (catalog).

Thirteen North American and two European species can be assigned with confidence to *Parallelodiplosis*. Five other species, four of them from India and the other from Hawaii, are presently placed in this genus, but their placement has yet to be confirmed. Although the biology of most species is unknown, larvae of several are inquilines in galls of insects of various orders (Gagné 2004, 2008, 2010). The adult character shared by the North American and European species is the horizontal division of the second through sixth abdominal tergites between the posterior and lateral setae. In addition, papillae of the terminal larval segment are of three distinct kinds: one pair large-corniform, pigmented, and recurved anteriorly; one pair with elongate setae; and two pairs with short-corniform setae. It is not known whether the Indian and Hawaiian species share these character states.

Parallelodiplosis acernea (Felt)

acernea Felt 1907: 46 (*Cecidomyia*); Felt 1908: 411 (*Clinodiplosis*); Felt 1915a: Plate 2, Fig. 12 (*Parallelodiplosis*), larva from illustrated galls misidentified as this species; Felt 1921: 167, formal description; Moser 1965: 17, first host record.

rubroscuta Felt 1907: 46 (*Cecidomyia*); Felt 1908: 411 (*Clinodiplosis*, as *rubrascuta*); Felt 1921: 165, formal description (*Parallelodiplosis*, as *rubrascuta*). **New synonym.**

nixoni Felt 1908: 414 (*Cecidomyia*); Felt 1921: 192, formal description (*Itonida*); Gagné 1973: 876 (*Parallelodiplosis*). **New synonym.**

Description.—*Adult*. **Head** (Fig. 107): Eyes connate, 11–12 facets long at vertex; facets hexagonal, all closely adjacent. Occiput with dorsal protuberance with 2 strong and elongate apical setae. Frons with 6–10 setae. Labellum ellipsoid, pointed apically, with several lateral setae. Palpus 4-segmented, with prominent palpiger. Male antennal flagellomeres (Figs. 107–108) binodal, distal node of each constricted near basal third; distalmost flagellomere with elongate, constricted terminus; 1 many-looped circumfilum present on basal node of each flagellomere, 2 on distal; loops of circumfila subequal in length, long, but not quite reaching next distal circumfilum. Female flagellomeres (Figs. 109–110) successively shorter from base to apex of antenna, the 2 first flagellomeres constricted and elongated between basal setae and basal band of circumfilum, remaining flagellomeres evenly cylindrical, the last with elongate, constricted terminus; each flagellomere surrounded by two appressed circumfila connected by two longitudinal bands. **Thorax**: Wing hyaline; length: male 1.9–2.4 (n=10), female, 2.2–2.6 (n=10); R_5 strongly curved toward apex, joining C posterior to wing apex, Rs weak, Cu forked, M_{3+4} evident. Tarsal claws (Fig. 111) untoothed, strongly curved beginning near mid-length; empodia as long as claws; pulvilli ca. 1/3 length of empodia. **Male abdomen**: First tergite short, sclerotized only along posterior margin, with mostly single row of posterior setae; second through sixth tergites horizontally variably indented laterad between posterior and lateral setae, unpigmented on basal third, with anterior pair of trichoid sensilla, mostly single row of posterior setae continuous across sclerite, several lateral setae, and sparse, scattered scales on pigmented portion; seventh and eighth tergites sclerotized only posterolaterally, seventh with anterior pair of trichoid sensilla, usually without lateral setae and with 2–4 posterior setae, the eighth without long setae, the only vestiture the anterior pair of trichoid sensilla. Second through eighth sternites pigmented only on posterior two-thirds, anterior pair of papillae situated on basal, membranous third, setae present along posterior margin and on mid-length of sclerite. Terminalia (Fig. 112): cerci with posterior margin concave, longer on lateral than mesal angle, with a single seta on mesal angle and 3 on lateral angle, one larger than the other two; hypoproct narrow and much longer than cerci, parallel-sided, nearly as wide as aedeagus, with 4 setae on posterior margin, and

covered with long setulae on both dorsum and venter; aedeagus elongate, longer and slightly wider than hypoproct, rounded apically; gonocoxite elongate-cylindrical, moderately splayed, angular basomedially; gonostylus elongate-cylindrical, with setulae near base and covered beyond with minute carinae and widely scattered short setae. **Female abdomen** (Figs.113–114): First through sixth tergites as for male; seventh tergite fully and evenly pigmented with anterior pair of trichoid sensilla, mostly single row posterior setae, several lateral setae, and scattered scales on posterior half; eighth tergite 1/2 as long and wide as seventh, an anterior pair of trichoid sensilla the only vestiture. First through sixth sternites as in male; seventh sternite fully pigmented, ca. 2× as long as sixth, with anterior trichoid sensilla and covered along entire length with setae and setiform scales; eighth sternite not apparent. Ovipositor slightly protrusible, extended eighth segment with setae posteroventrally, ninth segment with scattered setae laterally and ventrally, without setae dorsally, cerci elongate-ovoid, with pair of strong apical setae differentiated from those scattered elsewhere; ninth segment and cerci together ca. 1¼ length of seventh tergite; hypoproct short, narrow, with 2 short, posterior setae.

Pupa. Head: Antennal base rounded apically, not conspicuously projecting anteriorly; cervical sclerite with two elongate setae; face without ventral protuberances, with pair of closely placed papillae at each side near base of frons, one of them with seta, and closely placed triplet of papillae at base of each palpus, one of them with seta. Prothoracic spiracle elongate, pointed apically. Abdominal second through seventh tergites with row of strong anterior spines anteriorly, elsewhere evenly covered with uniformly small, pointed spicules.

Larva. **Third instar** (Figs. 179, 181): Length, 2.3–2.9 mm. Red. Integument mostly covered with pebbled verrucae, often pointed posteriorly, anterior half of venter on most segments minute-spiculose. Antenna less than 2× as long as wide. Spatula (Fig. 179) clove-shaped, elongate, broadest anteriorly, the 2 teeth broadly rounded and deeply divided. Lateral thoracic papillae in 2 groups of 3 on each side of thoracic segments, 2 papillae in each group with tiny seta, the third papilla slightly larger and without seta. Dorsal and pleural papillae with prominent, elongate setae. Terminal segment (Fig. 181) with 8 papillae as follows: 1 pair large-corniform, pigmented, slightly recurved anteriorly; 1 pair setose, the setae as long as dorsal setae of previous segment; 2 pairs, one behind the other, short-corniform, the anteriormost pair slightly the larger.

Type material.—*Cecidomyia acernea*: *Holotype*: ♂, Nassau, New York, VI-14-1906, taken on red maple, #267, E.P. Felt, deposited in NYSM.

Cecidomyia rubroscuta: *Holotype*: ♂, Albany, New York, VI-1-1906, taken on ash, #93, E.P. Felt, deposited in NYSM.

Cecidomyia nixoni: *Holotype*: ♂, Albany, New York, VII-6-1906, taken on New Jersey tea, #510, E.P. Felt, deposited in NYSM.

Remarks.—*Parallelodiplosis acernea*, originally known from a single specimen caught by sweeping (Felt 1907), was later reported from psyllid galls on hackberry by Moser (1965). That identification was made by the late George C. Steyskal of the Systematic Entomology Laboratory, USDA, and is reconfirmed. Three other Nearctic species of *Parallelodiplosis* are reported here as identical to *P. acernea*. These are *P. rubroscuta*, *P. nixoni* and *P. florida*, each described by Felt from a single male. The first two were also caught by sweeping vegetation in New York and are synonymized here. The third species, *P. florida*, was described from a single male reared from a pocket-like, midrib leaf swelling made by an undetermined cecidomyiid on an oak in Georgiana, Florida (Felt 1908). This third species is not synonymized at this time. It should be possible eventually to find larvae in similar oak galls that could then be compared to those of *P. acernea* to see whether they are distinct.

Affinities.—*Parallelodiplosis acernea*, *Parallelodiplosis florida* (Felt), and *Parallelodiplosis caryae* (Felt) are the only American species with tarsal claws that are curved beyond their mid-length. Empodia of the first two species, possible synonyms, are fully as long as the claws, while those of the third species are only slightly longer than 1/2 the length of the claws (Gagné 2008). The larval spatula of *P. acernea* (Fig. 179) is appreciably broader and has much more deeply divided anterior teeth than does that of *P. caryae* (Figs. 180). The larva of *P. florida* is unknown.

Biological notes.—Larvae of this species are fatal inquilines in hackberry galls made by cecidomyiids and at least two species of *Pachypsylla* (Moser 1965). During the present study larvae of *P. acernea* were found in galls of *C. aciculata*, *C. acuminata*, *C. capsularis*, *C. celtiphyllia*, *C. connata*,

C. expulsa, *C. oviformis*, *C. semenrumicis*, *C. spiniformis*, *C. subulata*, *C. supina*, and *Peracecis fugitiva*. The red larvae imparted a reddish cast to the normally green exterior of *C. aciculata* and *C. spiniformis* galls. Adults were reared from pots containing galls of *C. connata*, *C. expulsa*, *C. aciculata*, and *P. fugitiva*, and Moser (1965) reared adults from galls of *C. spiniformis*.

Larvae are orange to red, active when disturbed, and can be found inside galls of various species of *Celtcecis* and *P. fugitiva* from late April to October. They are usually in the presence of but separate from the moribund and otherwise seemingly undamaged larva responsible for the gall. Their food appears to come directly from the gall. Usually they occur singly in *Celticecis* galls, but occasionally two can be found, and three were once found in a gall of *C. expulsa* with the moribund *Celticecis* larva lying off to one side in the larval chamber. Its form of entry into the gall is unknown. In some cases an affected gall may have a hole through which a *Parallelodiplosis* larva possibly could have entered, but more often no hole or damage is apparent that would allow these larvae to enter the larval chamber. Possibly *P. acernea* lays its eggs in proximity to those of its associate and the gall subsequently grows around both. Emergence of *P. acernea* adults overlapped or lagged shortly behind that of *Peracecis fugitiva*, in whose galls *P. acernea* was commonly found. Adults of *P. fugitiva* emerged between March 9–27 and those of *P. acernea* between March19 and April 7, which suggests that the galls of the host may not yet be closed by the time the *Parallelodiplosis* females lay their eggs.

Collections and specimens of *P. acernea* examined.—**Florida**: Fort Pierce, V-26-2010, K.M. Hibbard, 2 larvae ex galls of *C. aciculata*; Fort Pierce, IV-14-2009, K.M. Hibbard, larva ex gall of *C. capsularis*. **Kentucky**: Lexington, V-28-2009, L. Rieske, 2 larvae ex galls of *C. acuminata*. **Louisiana**: Alexandria, IX-5-2010, JCM, 2 larvae ex galls of *C. spiniformis*; VII-5-2010, JCM, larva in gall of *C. subulata*; V-3-2010, JCM, 2 larvae ex galls of *C. semenrumicis*; IX-21-2008, JCM, larva ex galls of *C.aciculata*; VI-21-2009, JCM, 4 larvae ex galls of *C.aciculata*; VIII-7-2009, JCM & RJG, 3 ♂, emerged III-17-2010, ex galls of *C. aciculata*; V-16-2010, JCM, 3 larvae and ♀, emerged III-5-2011, ex galls of *C. connata*; 4 larvae, V-9-2010, JCM, ex galls of *C. oviformis*; V-3-2010, JCM, 2 larvae and 3 ♀, emerged IV-2–12-2011, ex galls of *C. expulsa*; IV-25-2010, JCM, 3 larvae and 18 ♂, 13 ♀, 4 pupal exuviae, emerged III-19 to IV-7-2011, ex galls of *P. fugitiva*; XII-15-1968, JCM, 2 larvae ex galls *Pachypsylla celtidismamma* Riley (Hemiptera: Psyllidae). **New York**: Albany, holotypes of *P. rubroscuta* and *P. nixoni*; Ithaca, 1957, JCM, 2 ♂, 1 ♀ ex *Pachypsylla celtidismamma* Riley (Hemiptera: Psyllidae); 1957, JCM, 2 larvae ex *Pachypsylla celtidisvesicula* Riley (Hemiptera: Psyllidae); Nassau, holotype of *P. acernea*. **North Carolina**: Wake Co., IX-6-1956, B.D. Wells, larva, ex galls *P. celtidisvesicula*. **Ohio**: Union, VI-22-2010, RJG, 3 larvae ex galls of *C. spiniformis*. **Texas**: near Lufkin, X-22-2009, JCM, 2 larvae ex galls of *C. aciculata*; Temple, IV-27-2010, T.O. Robbins, 2 larvae ex galls of *C.oviformis*; Temple, IV-28-2010, T.O. Robbins, 2 larvae ex galls of *P. fugitiva*. **West Virginia**: Falling Waters, VII-21-2009, RJG, 2 larvae ex galls of *C. celtiphyllia* and larva ex gall of *C. supina*.

GALL MIDGES ON *CELTIS* REPORTED OUTSIDE NORTH AMERICA

Celticecis japonica Yukawa & Tsuda, 1987. This species is known from Honshu and Kyushu in Japan on *Celtis* (*Celtis*) *sinensis* var. *japonica* (Planch.) Nakai and *Celtis* (*Celtis*) *jessoensis* Koidz. It forms an ovoid-conical, thin-walled stem and leaf-vein gall. A color photo of the gall is given in Yukawa & Masuda (1996). *Celticecis japonica* was discussed earlier in this paper under the generic description for its plesiomorphic character states, chiefly the short ovipositor and nearly full complement of larval papillae. SEMs are provided here of the remarkable female postabdomen (Figs. 62–65).

Celticecis sp. (Gagné & Moser 1987). This undescribed species is known from leaf galls (Figs. 49–50) of *Celtis tournefortii* Lam. collected in Hisarcik, Turkey. The galls we have seen are young, as evidenced by the very small second instars found inside them, but appear to be integral to the leaf. Perhaps they eventually form the same kind of dehiscent plug seen in galls of *C. expulsa* (Figs. 19–21). Galls similar to those on *C. tournefortii* were also noted on leaves of *Celtis glabrata* Steven ex Planch from Turkey (K. Browicz, *in litt.*). Second instar larvae excised from galls on *C. tournefortii* are too indistinct for description but do have a spatula, a trait of almost all second instars of *Celticecis*.

Neolasioptera celtis Möhn, 1964. Larvae were found in longitudinal tunnels inside spheroidal stem swellings of *Celtis iguanaea* in El Salvador. Felt (1940, 1965) listed a *Lasioptera* sp. (larvae of *Lasioptera* and *Neolasioptera* can be indistinguishable) from a "subcortical twig swelling" on *Celtis* sp. but without locality data. We have never noticed such swellings on *Celtis* (*Celtis*) in the U.S.

Other than the few species listed directly above, galls from Japan and several galls from the Neotropics attributed to cecidomyiids have been noted in publications. The gall midges of most of these were not collected or mentioned further beyond their initial notice, but some are illustrated with color photographs. The galls are as follows:

Leaf galls from Japan presumably formed by *Celticecis* spp. Two were mentioned in Moser (1965). One generally similar to the gall of *C. spiniformis* is probably that of *C. japonica*; the other was a winged gall "similar in appearance and position of attachment" to the galls of *C. semenrumicis*. A color photo of a further leaf gall on *Celtis boninensis* Koidz. is shown in Yukawa & Masuda (1996).

Spherical stem swelling. This evenly globular swelling, many times wider than the stem, was found on *Celtis brasiliensis* (Gardner) Planch. in Serra do Cipó, Minas Gerais, Brazil (Coelho *et al.* 2009). We note that *N. celtis* above also came from a spherical stem gall.

Spindle-form stem gall. Tapered stem swellings were found on *Celtis glycycarpa* Mart. ex Miq., Serra de São José, Tiradentes, Minas Gerais (Maia & Fernandes 2004) and on *Celtis brasiliensis* (Gardner) Planch. in Serra do Cipó, Minas Gerais, Brazil (Coelho *et al.* 2009).

Blister leaf gall. Tavares (1925) described a gall from *Celtis* sp. found in 1911 in Nova Friburgo, Rio de Janeiro. He gave no illustration but the gall as described appears similar to that of *P. fugitiva* (Figs. 51–54). On the upper side of the leaf the gall is globular, ca. 4 mm in diameter, yellowish green, rough-textured, the wall membranous, thin, and covering a large cavity. The gall is apparent on the lower surface of the leaf only by a small, finely mucronate cap. Whether larvae were retrieved from the gall was not noted. Tavares (1925) listed the gall maker only as "*Cecidomyia* sp.," a name used as a catchall category at the time for cecidomyiids that were undetermined or undeterminable beyond the level of the subfamily Cecidomyiinae.

Complex spherical leaf gall. This yellow, hairy gall, apparently attached to a vein, was reported from *Celtis glycycarpa* from Serra de São José, Tiradentes, Minas Gerais, Brazil (Maia & Fernandes 2004).

Spherical leaf gall. A yellow-orange gall was found on *Celtis brasiliensis* (Gardner) Planch. in Serra do Cipó, Minas Gerais, Brazil (Coelho *et al.* 2009).

Mammiform gall on stems and leaves. These are generally conical and tapered apically. They were reported from *Celtis glycycarpa* from Serra de São José, Tiradentes, Minas Gerais, Brazil (Maia & Fernandes 2004). The galls might appear to belong to a *Celticecis* but Maia and Fernandes identified the gall maker as a *Neolasioptera* sp. Larvae from the galls that one of us (RJG) saw through the kindness of V.C. Maia are not *Neolasioptera* and belong instead to the supertribe Cecidomyiidi because they have two groups of three papillae on each side of the spatula and asetose eighth abdominal ventral papillae. It is possible that both a *Neolasioptera* and another cecidomyiid could occur together in such galls.

Conical stem gall. This soft but thorn-like green gall was reported from *Celtis brasiliensis* in Serra do Cipó, Minas Gerais, Brazil (Coelho *et al.* 2009).

Conical leaf gall. Narrowly conical green or red galls, apparently situated on leaf veins, were found on *Celtis iguanaea* in Serra do Cipó, Minas Gerais, Brazil (Coelho *et al.* 2009). The illustration in the paper (*ibid.*) shows some resemblance to galls of *C. cornuata*.

Blister leaf gall. The gall is fairly flat, discoid, hairless, and attributed to a cecidomyiid. It was found on *Celtis brasiliensis* in Serra do Cipó, Minas Gerais, Brazil (Coelho *et al.* 2009).

KEY TO GALLS OF CECIDOMYIIDAE ON NORTH AMERICAN HACKBERRIES

This is a key to hardened, mature galls. Immature galls of many species often look alike because they first grow lengthwise before broadening to their ultimate shape. All except one of the cecidomyiid galls on hackberries are complex and detachable. These complex galls ultimately dehisce with the larvae still inside. They may form aggregate galls, but each larva will be in a separate chamber. The one simple, integral cecidomyiid gall is a soft, convex swelling that usually contains gregarious larvae that when mature escape the gall through a special opening. All other North American non-cecidomyiid galls on hackberry are integral galls. Pristine cecidomyiid galls have no frass, wax or other detritus. The inhabitants are legless and their head capsules, except under strong magnification, are almost imperceptible. These features will separate them from other gallmakers of buds, stems and leaves that are formed mostly by Psyllidae (Hemiptera) but also by Eriophyidae (Acarina) and Agromyzidae (Diptera).

1. Simple, integral, convex leaf swelling, more prominent on lower leaf surface (Figs. 51–54) ..... *Peracecis fugitiva*
Complex, detachable galls on leaves, twigs or fruit (Figs. 1–48) ..... *Celticecis* spp. 2

2(1). On leaf, usually on underside and seldom causing distortion (Figs. 1–6) 3
On twig, bud, fruit, occasionally on leaf surface and then usually causing distortion to leaf (Figs. 13–15) 17

3(2). On leaf lamina between veins (Figs. 1–6) 4
Attached to vein (Figs. 17, 31) 12

4(3). Surface naked (Figs. 1–2) 5
Surface hairy Figs. 3–6) 9

5(4). Apex rounded, gall less than 2 mm in length (Fig. 18) ..... *C. cupiformis*
Apex pointed, gall more than 3 mm in length (Fig. 2) 6

6(5). Gall abruptly narrowed to a point near apex (Fig. 1) ..... *C. aciculata*
Gall gradually tapered to apex Figs. 39, 42) 7

7(6). Base strongly flared outwards (Fig. 39) ..... *C. spiniformis*
Evenly conical, gradually tapered from base to apex (Figs. 12, 42) 8

8(7). Barely longer than wide, less than 3 mm long (Figs.11–12) ..... *C. conica*
At least 5 times longer than wide, at least 5 mm long (Fig. 42) ..... *C. subulata*

9(4). Flat, circular, sides deeply sulcate (Figs. 5–6) ..... *C. capsularis*
Upright, sides not sulcate (Figs. 3–4, 18) 10

10(9). Barrel-shaped, less than 2 mm high, brown, with sparse hair (Fig. 18) ..... *C. cupiformis*
Conical or acuminate, more than 5 mm high, green, thickly haired (Figs. 4, 28) 11

11(10). Bulbous at base, acuminate towards rounded apex (Figs. 3–4) ..... *C. acuminata*
Evenly conical (Fig. 28) ..... *C. pilosa*

12(3). Situated in fork of major veins (Figs. 29–30, 47–48) 13
Situated along any vein (Figs. 17, 23, 45) 14

13(12). Cylindrical (Figs. 29–30) ..... *C. pubescens*
Turbinate (Figs. 47–48) ..... *C. wellsi*

14(12). Situated atop vein on persistent pad (Figs. 16–17) ..... *C. cornuata*
Attached directly to vein, usually to side, without intervening pad (Figs. 22, 45) 15

15(14). Gall elongate-conical, supine (Figs. 44–46) ..... *C. supina*
Cylindrical or bulbous, usually upright (Figs. 22, 31) 16

16(15). Gall irregularly cylindrical (Figs. 31–32) ..... *C. pyriformis*
Gall spheroidal (Figs. 22–23) ..... *C. globosa*

17(2). Surface hairy (Figs. 7, 25) 18
Surface naked (Figs. 14, 37) 20

18(17). Evenly spherical with barely evident attenuated apex (Figs. 25–27) ..... *C. oviformis*
Cylindrical or ovate with long attenuate apex (Figs. 7, 24, 37) 19

19(18). Cylindrical, widest immediately below short, narrow, pointed apex (Figs. 7–10) ..... *C. celtiphyllia*
Ovate with gradually attenuate apex (Fig. 24) ..... *C. ovata*

20(17). Sides deeply sulcate, with 4 or more vertical winglike extensions (Figs. 36–38) ..... *C. semenrumicis*
Cylindrical or spherical, sides not sulcate (Figs. 14, 20, 34) 21

21(20). Spheroid, usually comprising two to many separate larval chambers (Figs. 13–15) ..... *connata*
Cylindrical, may be closely adjacent to one another but rarely completely joined (Figs. 20, 34) 22

22(21). Regularly cylindrical with abruptly attenuate apex, entire gall eventually separating from stem or leaf (Figs. 33–35) ..... *C. ramicola*
Irregularly cylindrical, tapering from wide base, the base integral with stem or leaf; only inner core containing larval chamber eventually dehiscing (Figs. 19–21) ..... *C. expulsa*

KEY TO LARVAE OF CECIDOMYIIDAE ON NORTH AMERICAN HACKBERRIES

This is a key to both second and third instar larvae of cecidomyiids that occur on hackberries in North America north of Mexico. These are: 21 species of *Celticecis*, *Peracecis fugitiva*, *Parallelodiplosis acernea* and *Lestodiplosis* sp. The last species, a predator, is undetermined further and known only from larvae. It was rarely found on hackberry galls during this study. It is included here but not treated elsewhere in this paper.

Use of the key will usually require a well-cleared, slide-mounted specimen and a compound microscope, preferably with phase contrast. Although galls are usually distinctive enough to separate most species, those of a few species can be confused. In those cases this key may serve as further corroboration for an identification.

1. Abdomen with spiracles on only the first thoracic and eighth abdominal segments ..... first instars, not keyed further
   Abdomen with spiracles on first thoracic and first through eighth abdominal segments 2

2(1). Antenna elongate, pointed, at least 4 times as long as basal width; a predator ..... *Lestodiplosis* sp.
   Antenna short-stubby, ca. 2× as long as basal width 3

3(2). Terminal segment with variously shaped papillae, one pair especially prominent, spinelike (Fig. 181) ..... *Parallelodiplosis acernea*
   Terminal segment with papillae all hairlike (Figs. 96, 106) 4

4(3). Terminal segment bilobed, each lobe with four apical setae (Fig. 106); 2 groups of 3 lateral papillae present on each side of thoracic segments ..... *Peracecis fugitiva*
   Terminal segment evenly convex, the 4–8 setae scattered (Fig. 96); usually 2, occasionally 3–4, lateral papillae present on each side of thoracic segments (Fig. 98, c) ..... *Celticecis* spp. 5

5(4). Integument spiculose (Fig. 150) ..... second instar larvae 6
   Integument mostly pebbled (Figs. 95–98) ..... third instar larvae 21

6(5). Spicules on each side of thoracic venter appreciably larger than elsewhere (as in Fig. 167) 7
   Spicules on each side of thoracic venter and elsewhere uniform in size 14

7(6). Spatula with two anterior teeth (Fig. 162) ..... *C. pilosa* (in part)
   Spatula with a single anterior tooth 8

8(7). Four dorsal papillae on thoracic and first through seventh abdominal tergites 9
   Six dorsal papillae on thoracic and first through seventh abdominal tergites 11

9(8). Spatula tooth appreciably shorter than shaft (Figs. 150–151) ..... *C. aciculata*, *C. acuminata*
   Spatula tooth subequal to or shorter than shaft (Figs. 152,155) 10

10(9). Spatula tooth longer than shaft (Fig. 155) ..... C. *cupiformis*
   Spatula tooth subequal to angular shaft (Fig. 152) ..... *C. capsularis*

11(8). Spatula shaft extending anteriorly on each side of tooth (Fig. 167) ..... *C. spiniformis*
   Spatula shaft evenly horizontal anteriorly (as in Fig. 169) 12

12(11). Spatula shaft rounded anteriorly (Fig. 154) ..... *C. conica*
   Spatula shaft angular anteriorly (Figs. 168–169) 13

13(12). Spatula tooth obtusely pointed (Fig. 169) ..... *C. supina*
   Spatula tooth acutely pointed (as in Fig. 168) ..... *C. pilosa* (in part), *C. subulata*

14(6). Spatula lacking ..... *C. cornuata*
   Spatula present 15

15(14). Spatula shaft weakly developed, subequal in length to tooth (Fig. 159) ..... *C. globosa*
   Shaft of spatula robust, appreciably longer than tooth 16

16(15). First through seventh abdominal segments with 1 pleural papilla on each side; terminal segment with 6 or fewer papillae 17
   First through seventh abdominal segments with 2 pleural papillae on each side; terminal segment with 8 papillae 18

17(16). Spatula shaft convex laterally (Fig. 170) ..... *C. wellsi*
   Spatula shaft concave laterally (Fig. 163–164) ..... *C. pubescens*, *C. pyriformis*

18(16). Lateral papillae with long setae, nearly the length of ventral papillae (as in Fig 160) . . . . . *C. ovata*, *C. ramicola*, *C. semenrumicis*
Lateral papillae with setae no longer than papillar basal width (as in Fig. 153) 19

19(18). Spicules on venter of collar segment tiny and much more crowded than elsewhere (Fig. 153) . . . . . *C. celtiphyllia*
Spicules on collar segment uniform throughout 20

20(19). Spatula tooth narrow, ca. 2× as long as wide (Fig. 161) . . . . . *C. oviformis*
Tooth of spatula broad, ca. as long as wide (Fig. 156–157) . . . . . *C. connata*, *C. expulsa*

21(5). Spatula barely evident (Figs. 130–131) 22
Spatula consisting of large shaft and prominent apical tooth or teeth 23

22(21). Anterior edge of spatula acute (Fig. 131) . . . . . *C. cupiformis*
Anterior edge of spatula obtuse (Fig. 130) . . . . . *C. capsularis*

23(21). Spatula with single tooth, subtended on each side by narrow anterior projection of shaft (Fig. 146) . . . . . *C. spiniformis* (in part)
Spatula with two teeth 24

24(23). Sternal papillae with setae (Fig. 136) . . . . . *C. cornuata*
Sternal papillae without setae (as in Fig. 137) 25

25(24). First through seventh abdominal segments with 2 sternal papillae 26
First through seventh abdominal segments with 4 sternal papillae 31

26(25). Thoracic and first through seventh abdominal segments with 4 dorsal papillae 27
Thoracic and first through seventh abdominal segments with 6 dorsal papillae 28

27(26). Spatula teeth widely separated (Fig. 128) . . . . . *C. aciculata*
Spatula teeth joined at base (Fig. 129) . . . . . *C. acuminata*

28(26). First through seventh abdominal segments with 2 pleural papillae on each side . . . . . *C. globosa*
First through seventh abdominal segments with 1 pleural papilla on each side 29

29(28). Spatula shaft extending appreciably laterad of teeth and angular (Fig. 149) . . . . . *C. wellsi*
Spatula shaft, if extending laterad of teeth, convex 30

30(29). Lateral papillae with setae apparent (Fig. 134) . . . . . *C. conica*
Lateral papillae without apparent setae (as in Fig. 145) . . . . . *C. pilosa*, *C. spiniformis* (in part), *C. supina*

31(25). Four dorsal papillae on thoracic segments; 1 pleural papilla on each side of first through seventh abdominal segments 32
Six dorsal papillae on thoracic segments; 2 pleural papillae on each side of first through seventh abdominal segments 34

32(31). Spatula shaft oval, wider than long (Fig. 148) . . . . . *C. subpatula*
Spatula shaft rectilinear, longer than wide 3

33(32). Spatula shaft rectangular, teeth as long as wide (Fig. 141) . . . . . *C. pubescens*
Spatula shaft trapezoidal, teeth 2× as long as wide (Fig. 142) . . . . . *C. pyriformis*

34(31). Lateral papillae with setae nearly as long as ventral papillae . . . . . *C. ovata*, *C. ramicola*, *C. semenrumicis*
Lateral papillae with setae no longer than width of papillar base 35

35(34). Spatula shaft deeply concave laterally (Fig. 132); setae of eighth abdominal segment 2× as long as spiracular width . . . . . *C. celtiphyllia*
Spatula shaft not concave laterally; setae of eighth abdominal segment subequal in length to spiracular width 36

36(35). Spatula shaft with triangular indentation between teeth (Fig. 139) . . . . . *C. oviformis*
Spatula shaft without triangular indentation between teeth 37

37(36). Spatula shaft with slight projection between teeth (Fig. 133). . . . . *C. expulsa*
Spatula shaft without projection between teeth (Fig. 135) . . . . . *C. connata*

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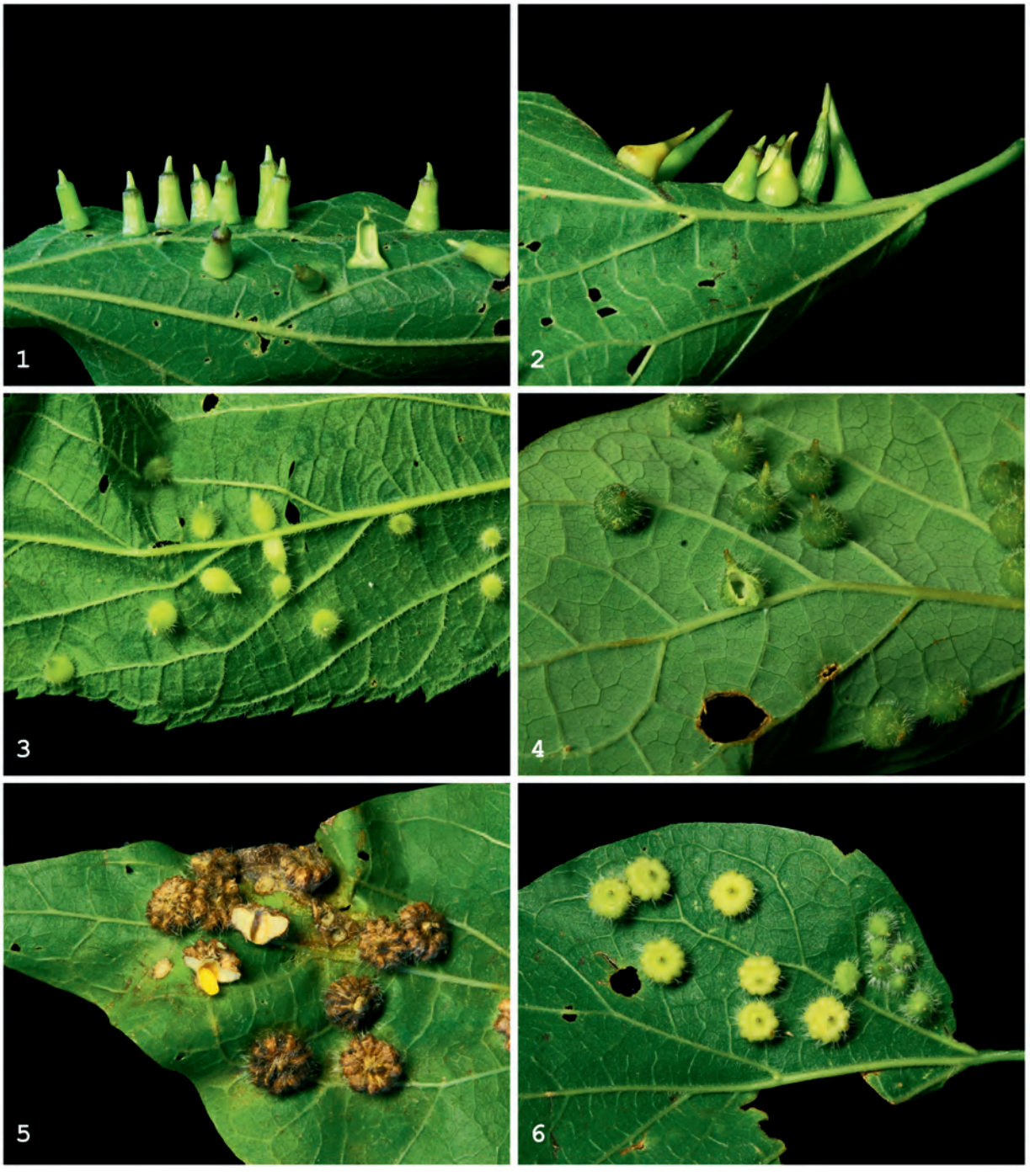
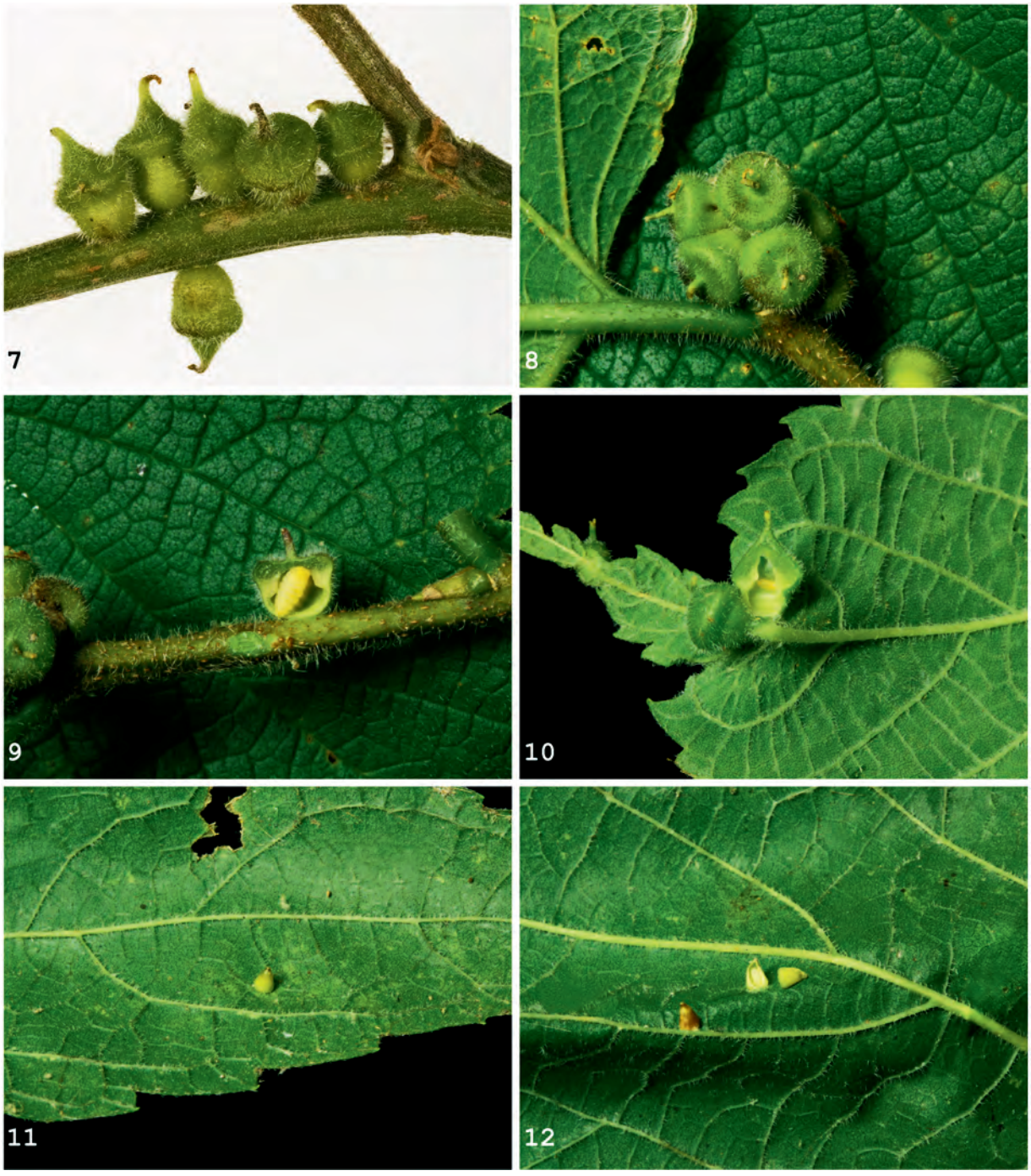
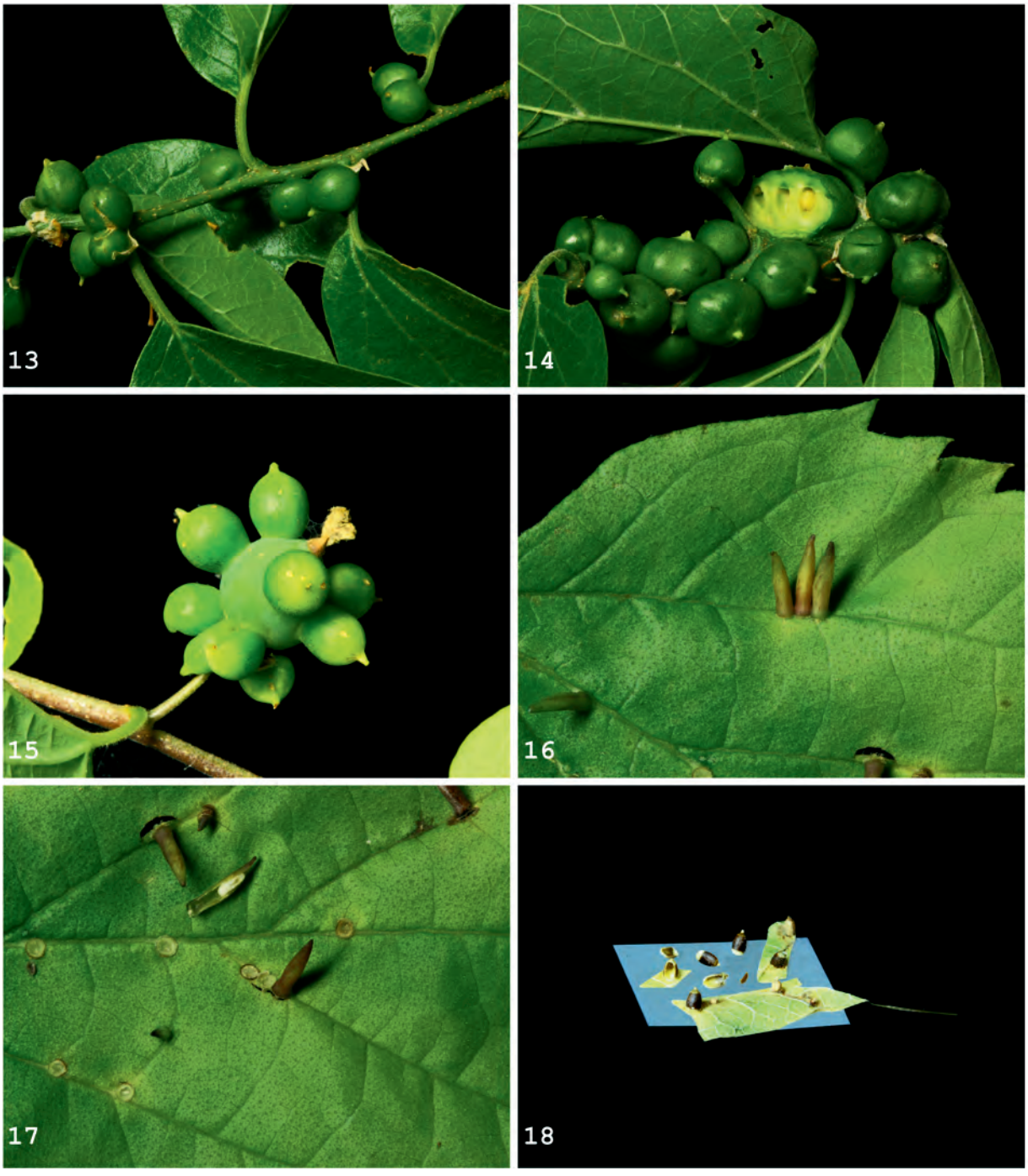


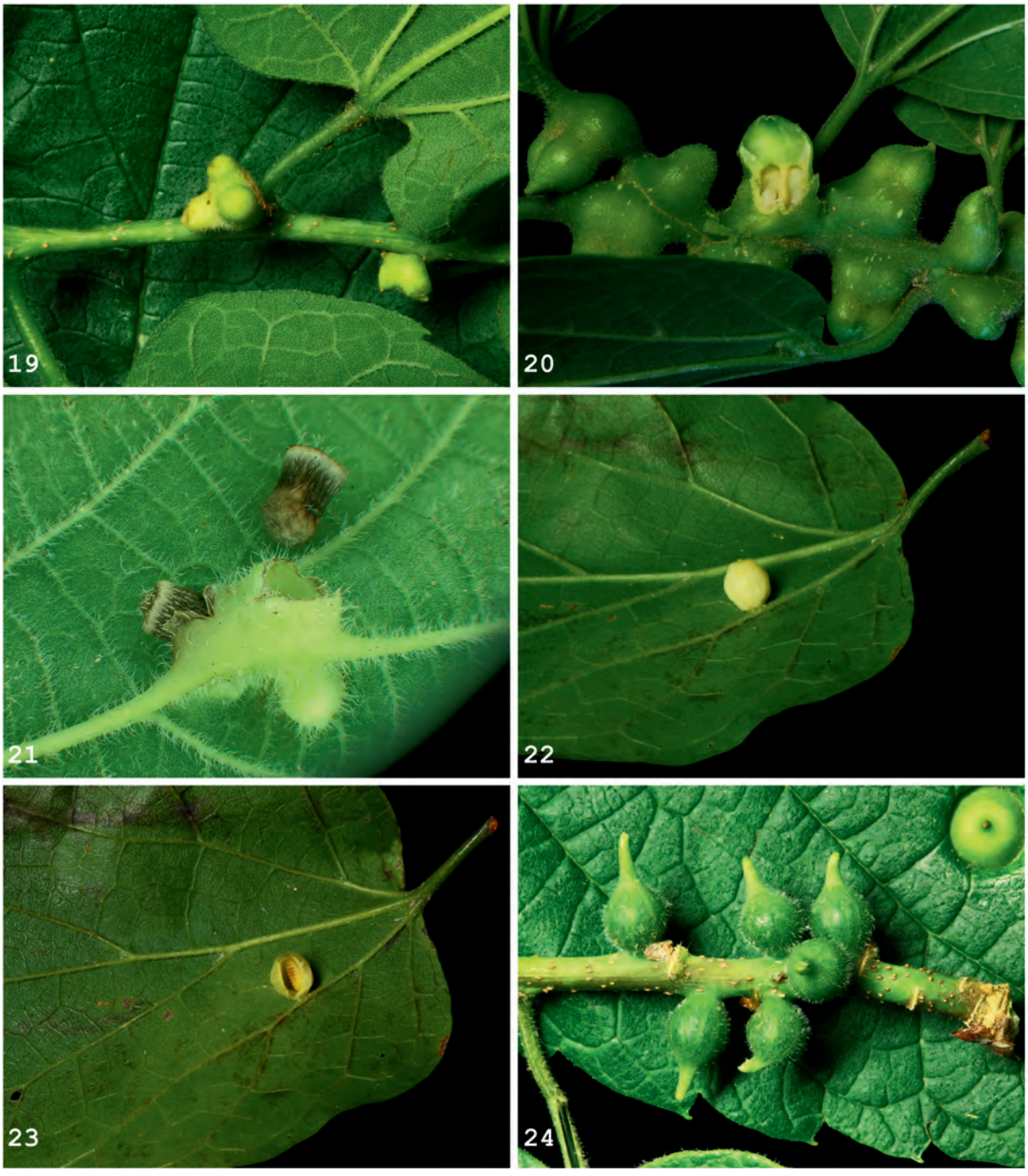
Figs. 1–6, *Celticecis* galls. 1, *C. aciculata*: group with one in section. 2, Assemblage of *C. aciculata*, *C. spiniformis* and *C. subulata*. 3–4, *C. acuminata*: 3, Young galls. 4, Mature galls, one in section with third instar. 5–6, *C. capsularis*: 5, Mature galls, one in section. 6, Young galls. All figures 2× actual size.



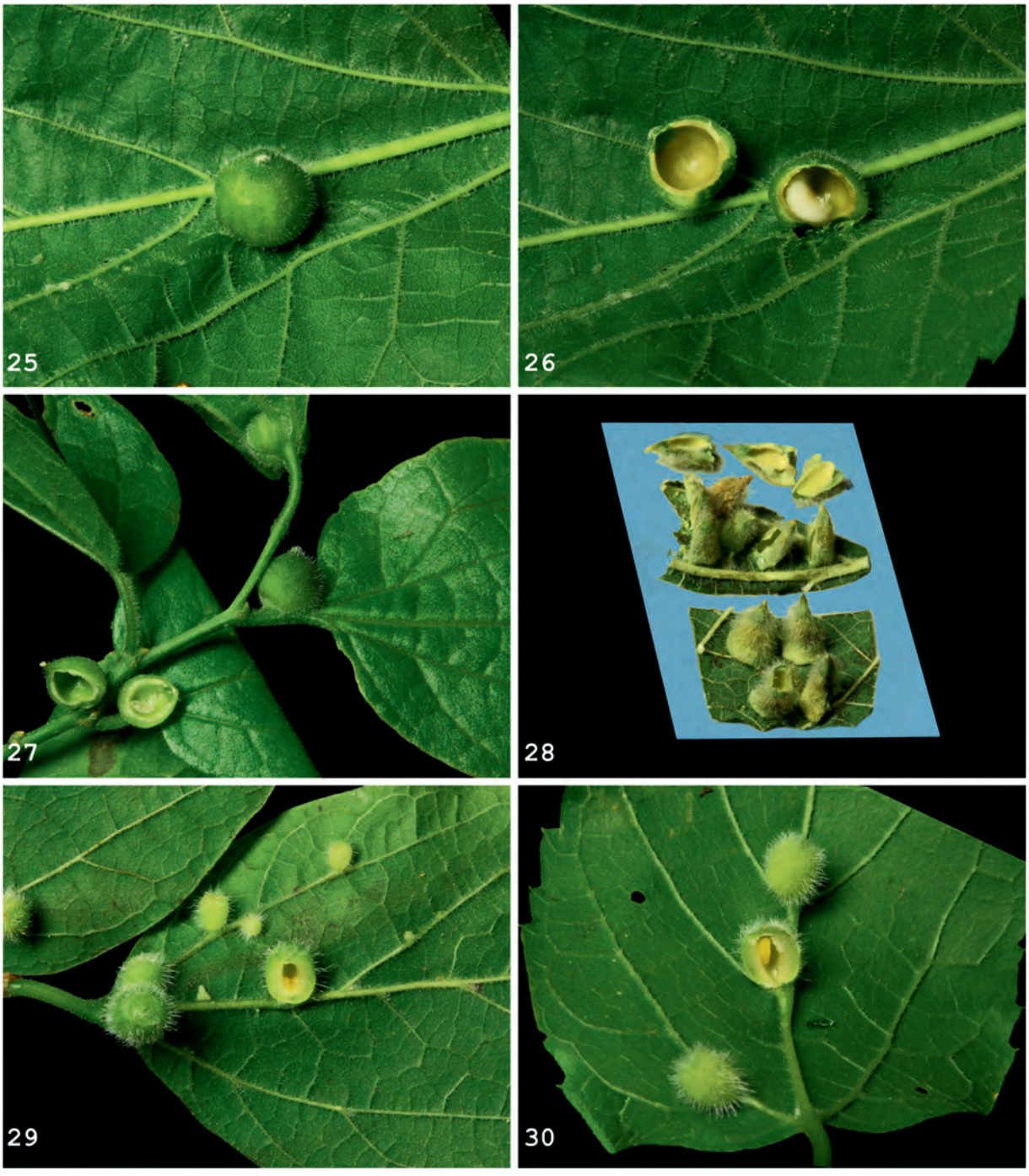
Figs. 7–12, *Celticecis* galls. 7–10, *C. celtiphyllia*: 7, Galls on twig. 8, Galls on leaf. 9, Mature gall in section with third instar. 10, Young gall in section with second instar. 11–12, *C. conica*: 11, Mature gall. 12, Gall in section with third instar. All figures 2× actual size.



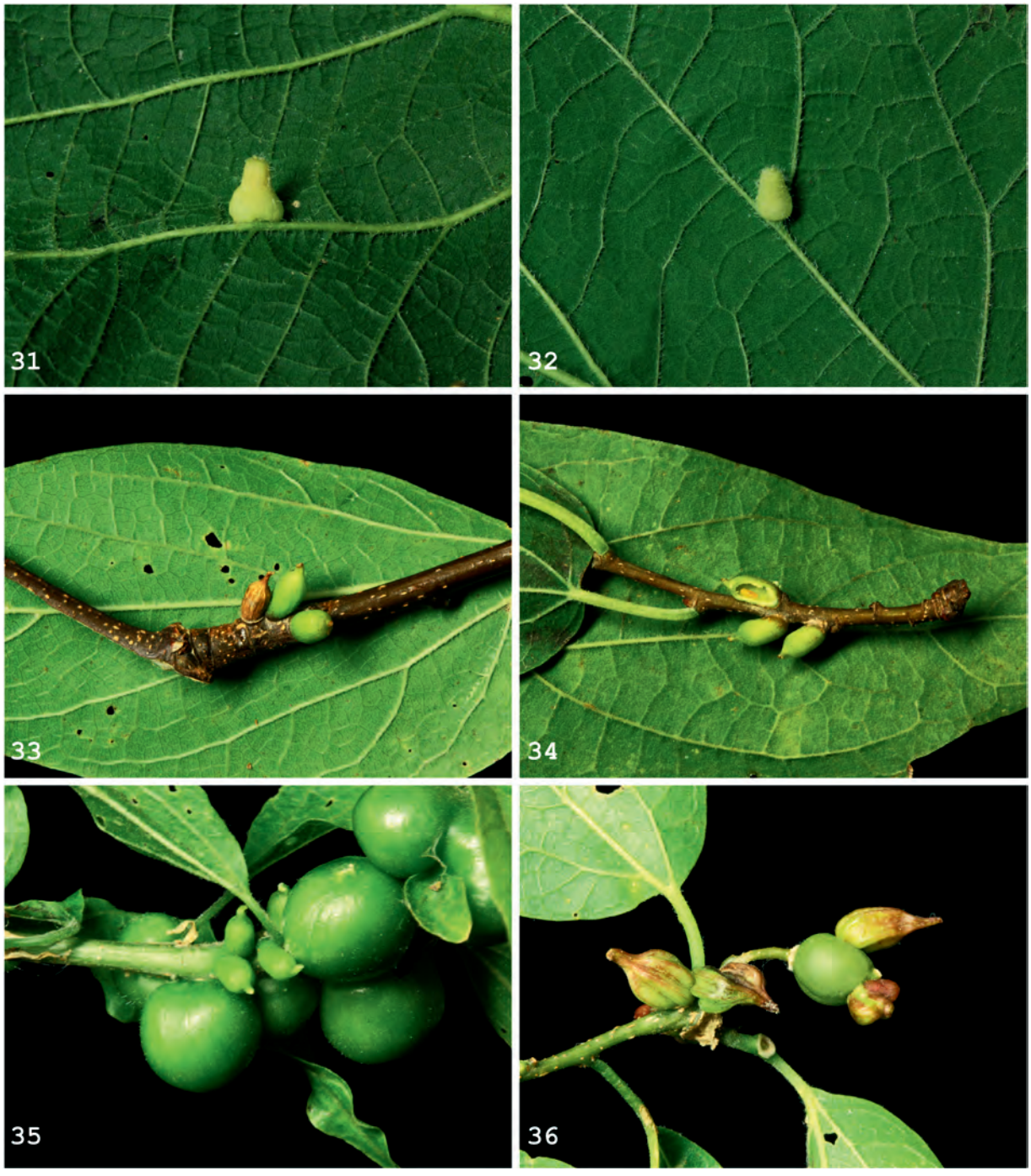
Figs. 13–18, *Celticecis* galls. 13–15, *C. connata*: 13, Galls on twig. 14, Composite gall in section with third instars. 15, Galls on fruit. 16–17, *C. cornuata*: 16, Galls in typical position along vein. 17, One in section with third instar (note pads left on veins after galls have dropped). 18, *C. cupiformis*: group with examples in section. All figures 2× actual size.



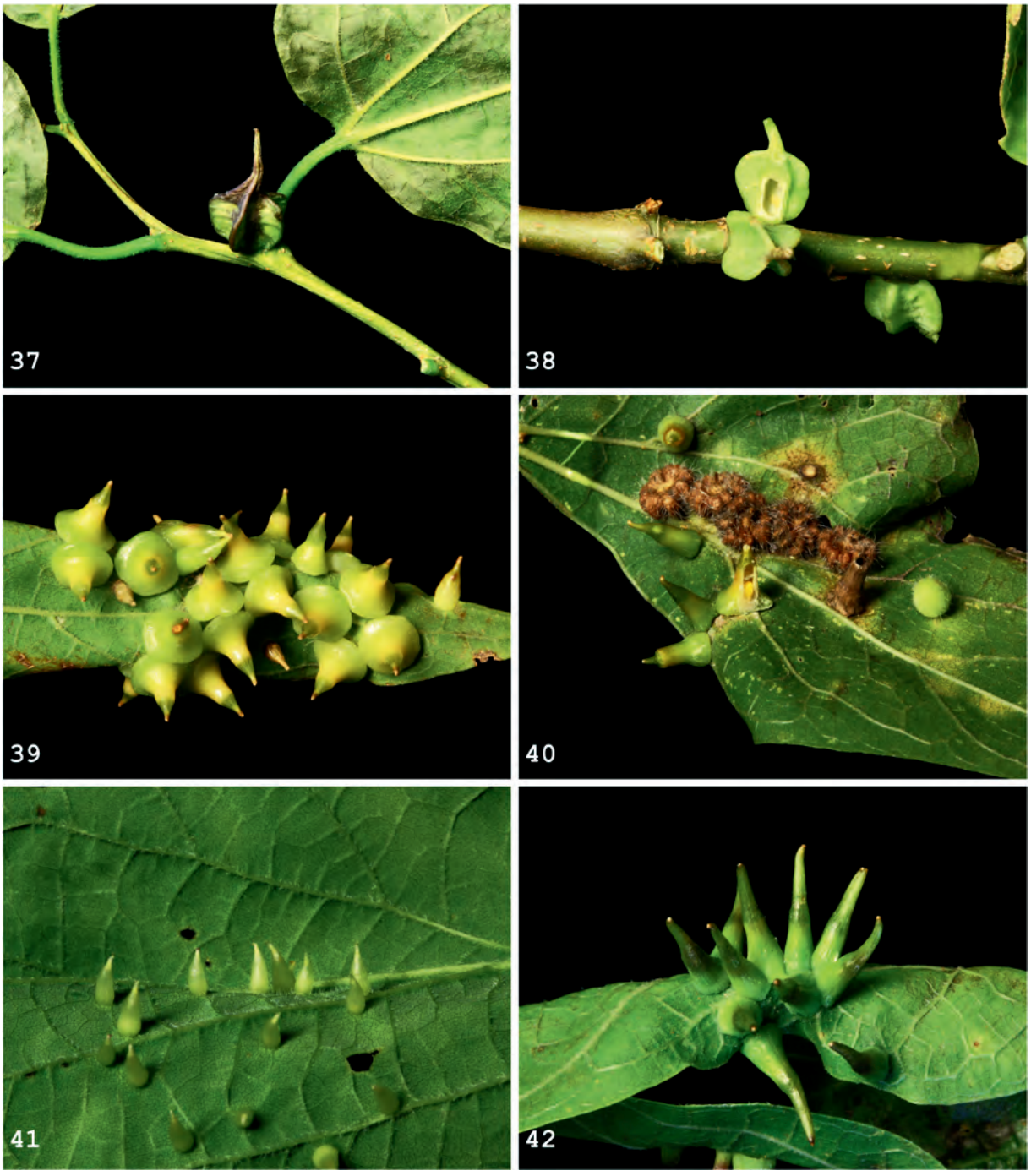
Figs. 19–24, *Celticecis* galls. 19–21, *C. expulsa*: 19, Young galls. 20, One aggregate gall in section with plugs beginning to form. 21, Mature galls with dehiscent larval chambers. 22–23, *C. globosa*: 22, Mature gall on leaf. 23, Gall in section with third instar. 24, *C. ovata*: Galls on twig, with psyllid leaf gall at upper right. All figures 2× actual size.



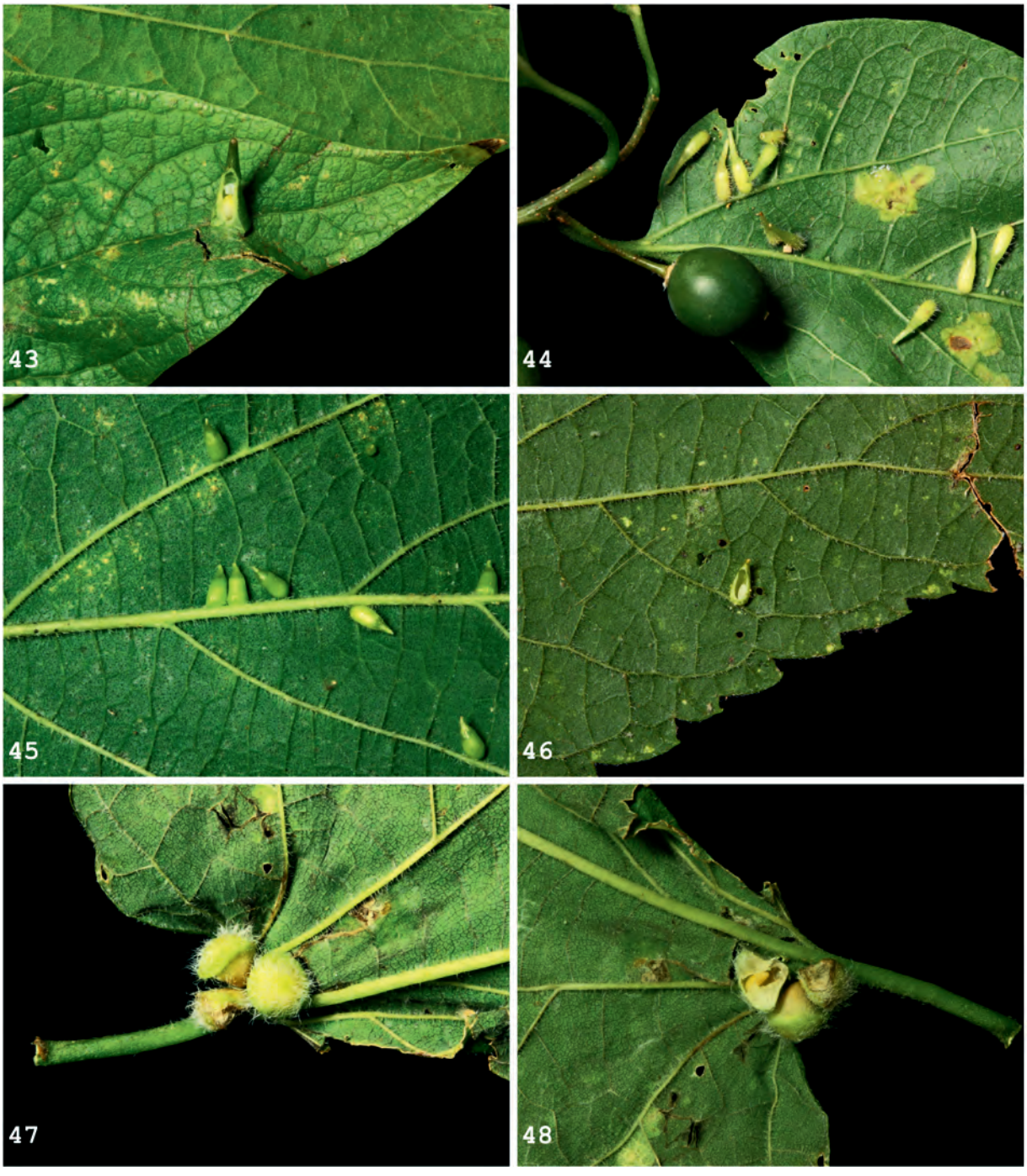
Figs. 25–30, *Celticecis* galls. 25–27, *C. oviformis*: 25, Mature gall on leaf lamina. 26, Gall in section with third instar. 27, Young galls, one in section with second instar. 28, *C. pilosa*: Group with examples in section. 29–30, *C. pubescens*: 29, Galls of various ages, one in section with third instar. 30, Mature galls, one in section with third instar. All figures 2× actual size.



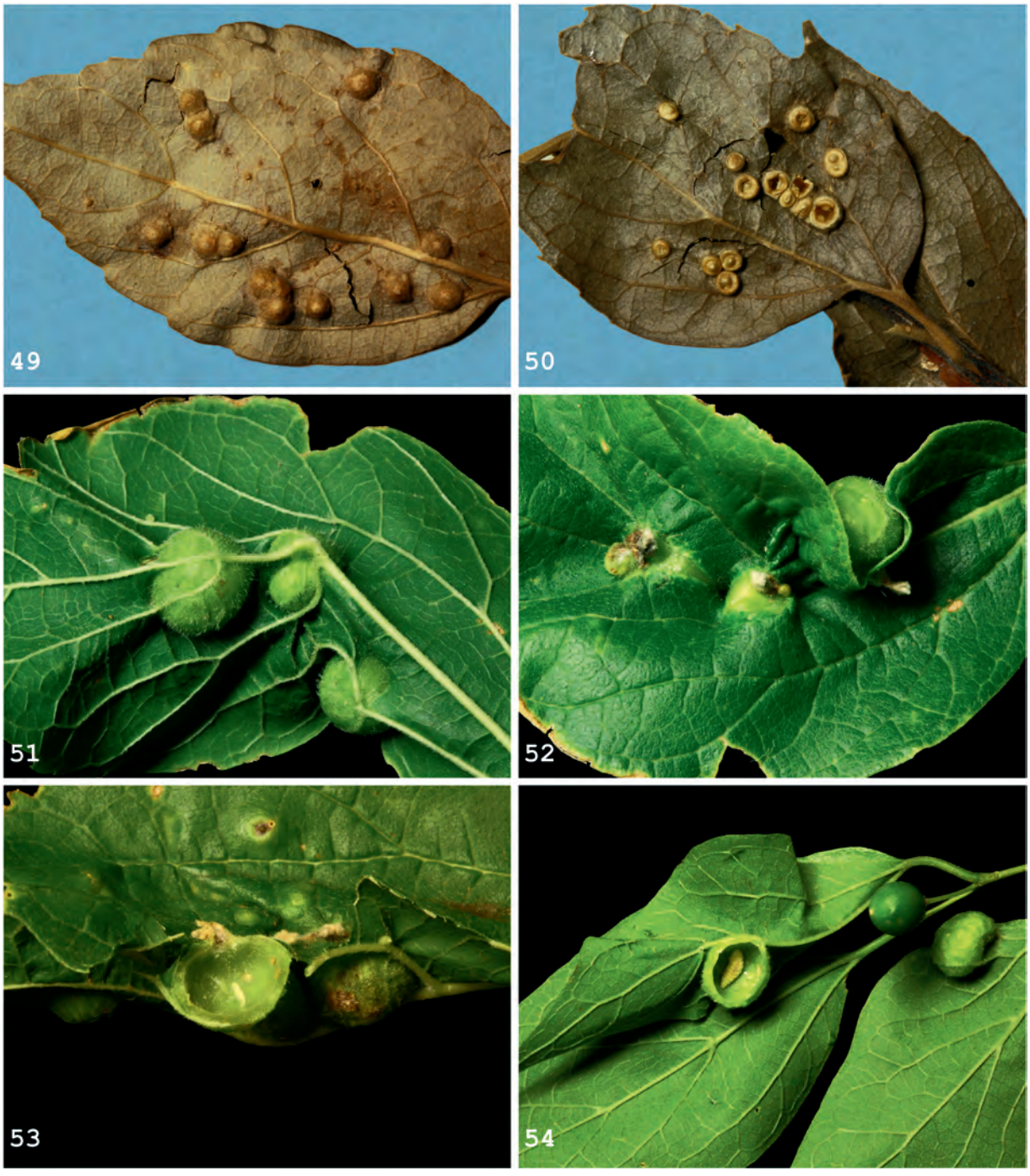
Figs. 31–36, *Celticecis* galls. 31–32, *C. pyriformis*: 31, Mature gall on vein. 32, Gall at typical position at vein fork. 33–34, *C. ramicola*: 33, Galls on twig. 34, Galls, one in section with second instar. 35, Assemblage of *C. ramicola* (smaller galls) and *C. connata*. 36, *C. semenrumicis*: Young galls, two growing from fruit. All figures 2× actual size.



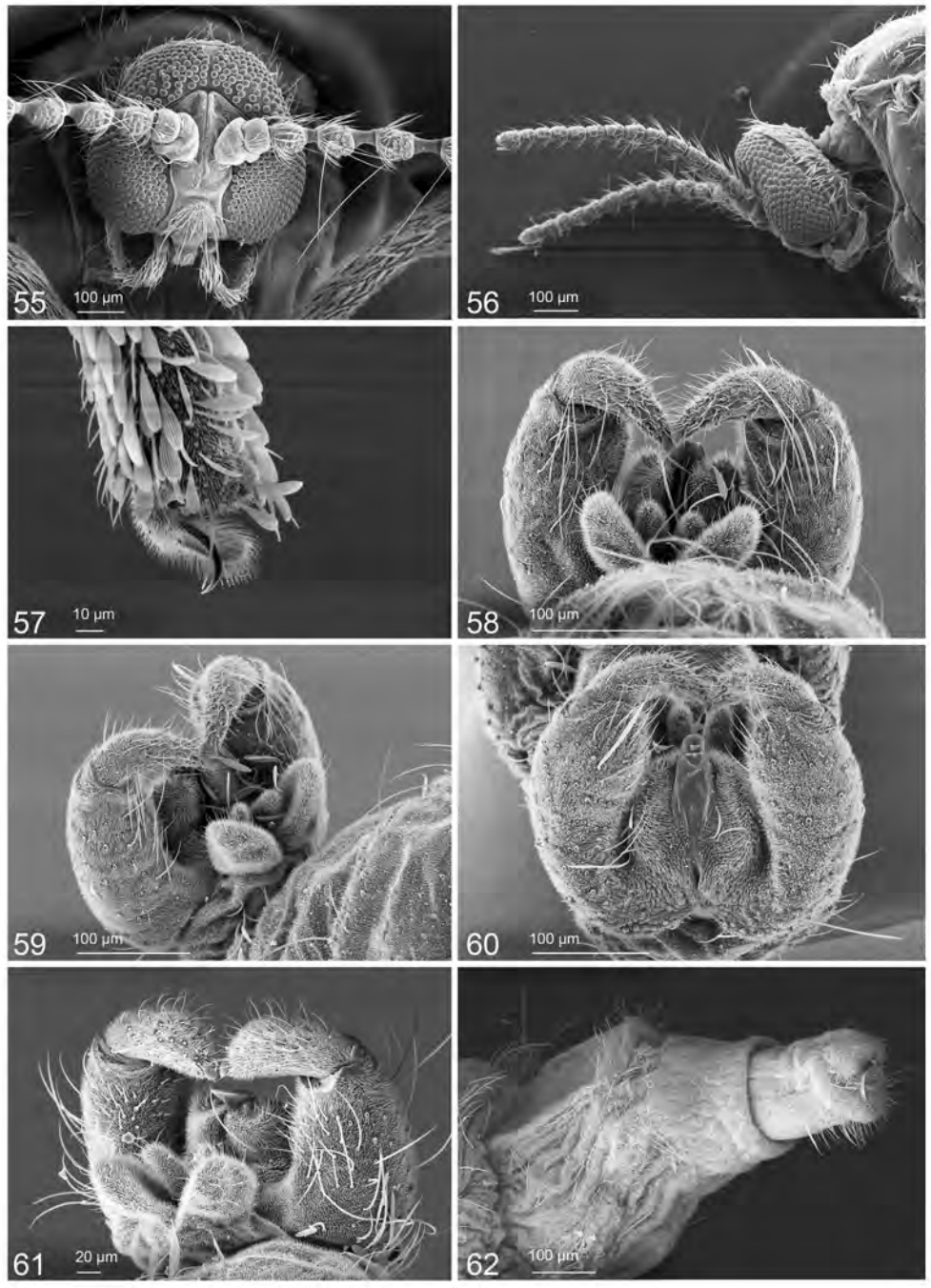
Figs. 37–42, *Celticecis* galls. 37–38, *C. semenrumicis*: 37, Four-winged specimen. 38, Gall in section. 39, C. *spiniformis*: Galls showing variation in shape. 40, Assemblage of galls made by *C. spiniformis* (including gall in center, sectioned, showing cocooned third instar), *C. aciculata*, *C. capsularis* and *C. globosa*. 41, *C. spiniformis*: Young galls. 42, *C. subulata*: Assemblage of galls distorting leaf. All figures 2× actual size.



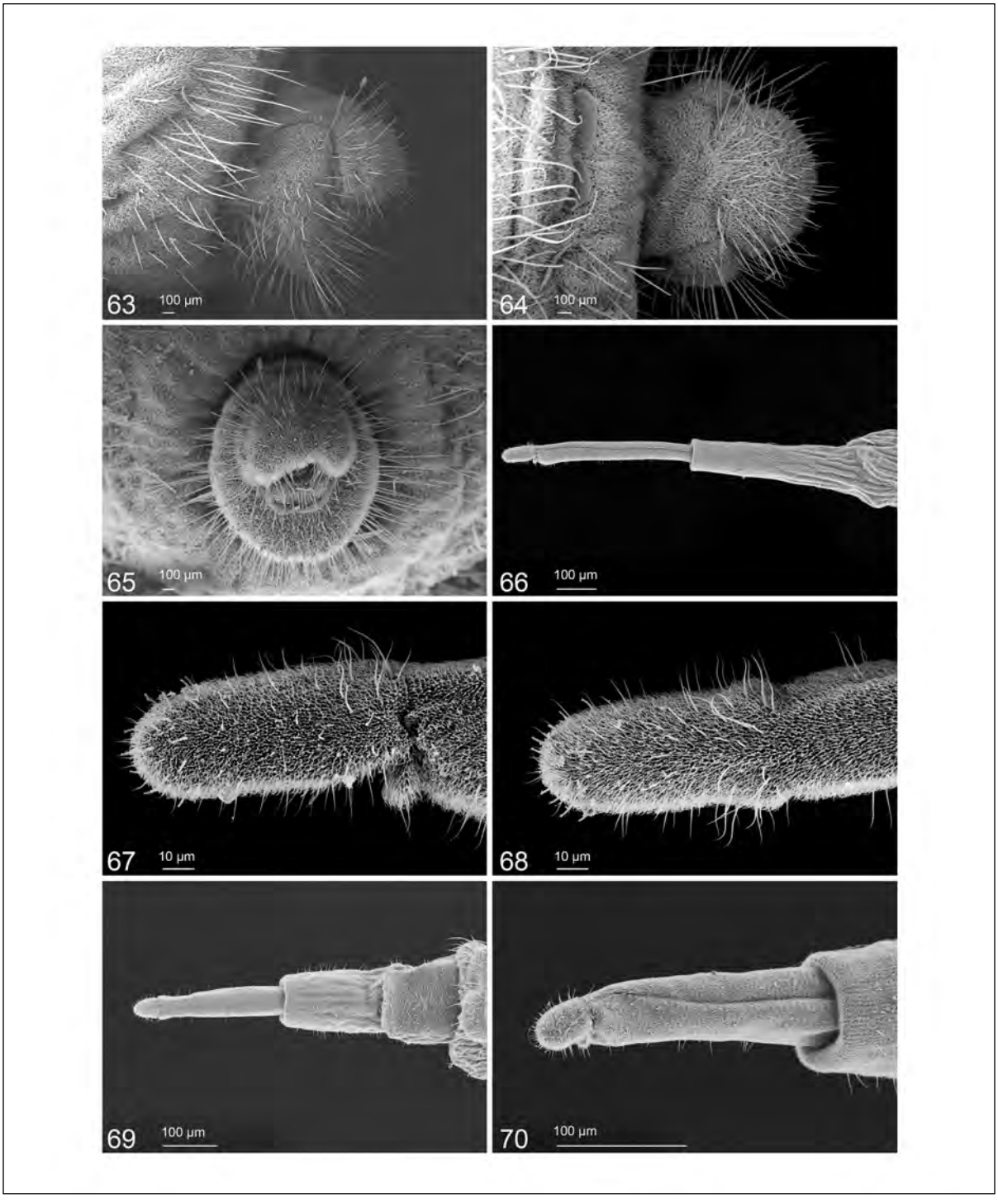
Figs. 43–48, *Celticecis* galls. 43, *C. subulata*: Gall in section with cocooned third instar. 44–46, *C. supina*: 44, Long-necked galls. 45, Short-necked galls. 46, Gall in section with third instar. 47–48, *C. wellsi*: 47, Galls in vein fork. 48, Gall in section with third instar. All figures 2× actual size.



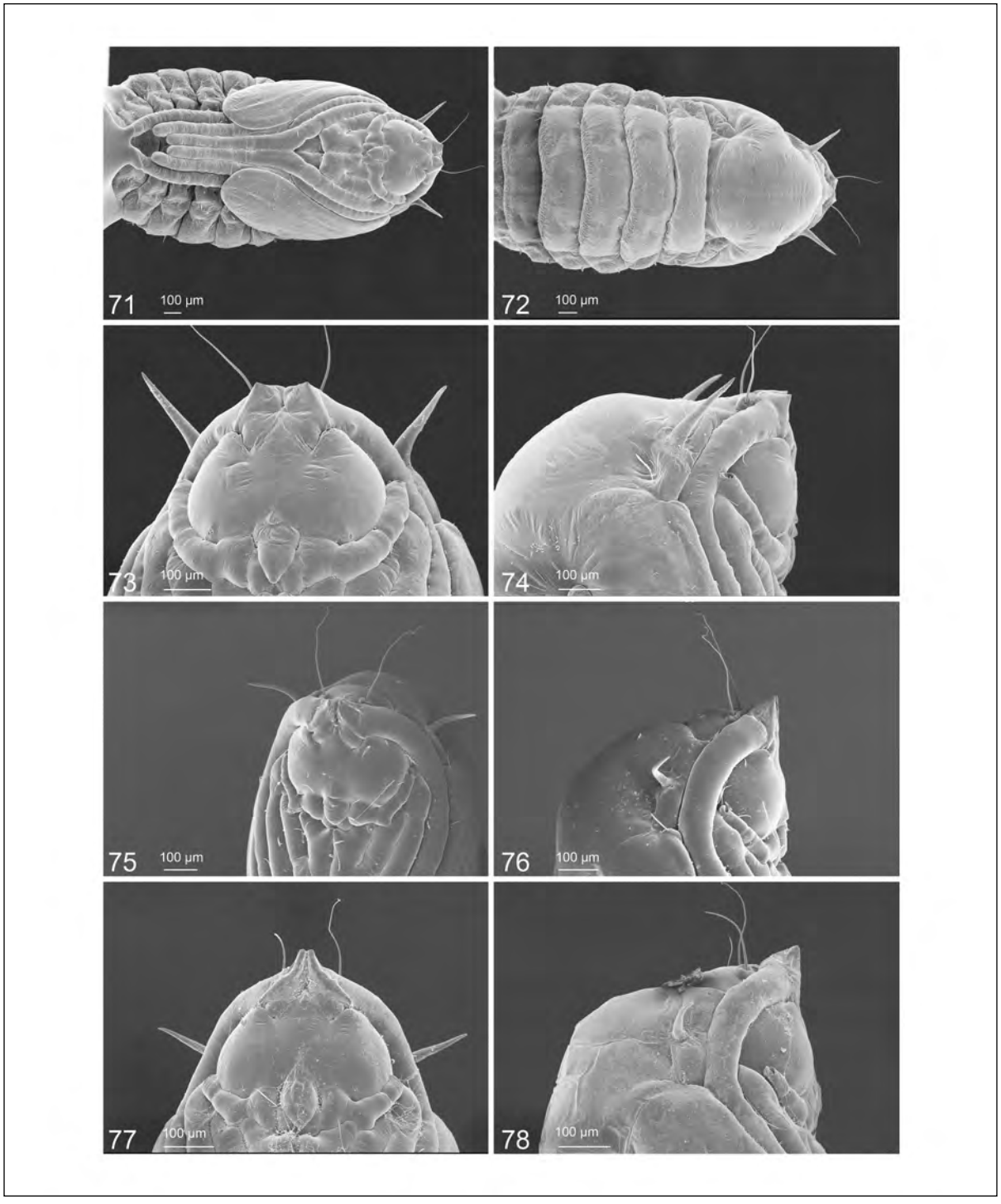
Figs. 49–54, Galls on *Celtis*. 49–50, *Celticecis* sp. galls of undetermined species from Turkey: 49, Bottom of leaf. 50, Top of leaf, some galls in section. 51–54, *Peracecis fugitiva* galls: 51, Bottom of leaf. 52, Top of leaf showing escape chimney. 53, Gall in longitudinal section. 54, Gall in cross section, with third instar. All figures 2× actual size.



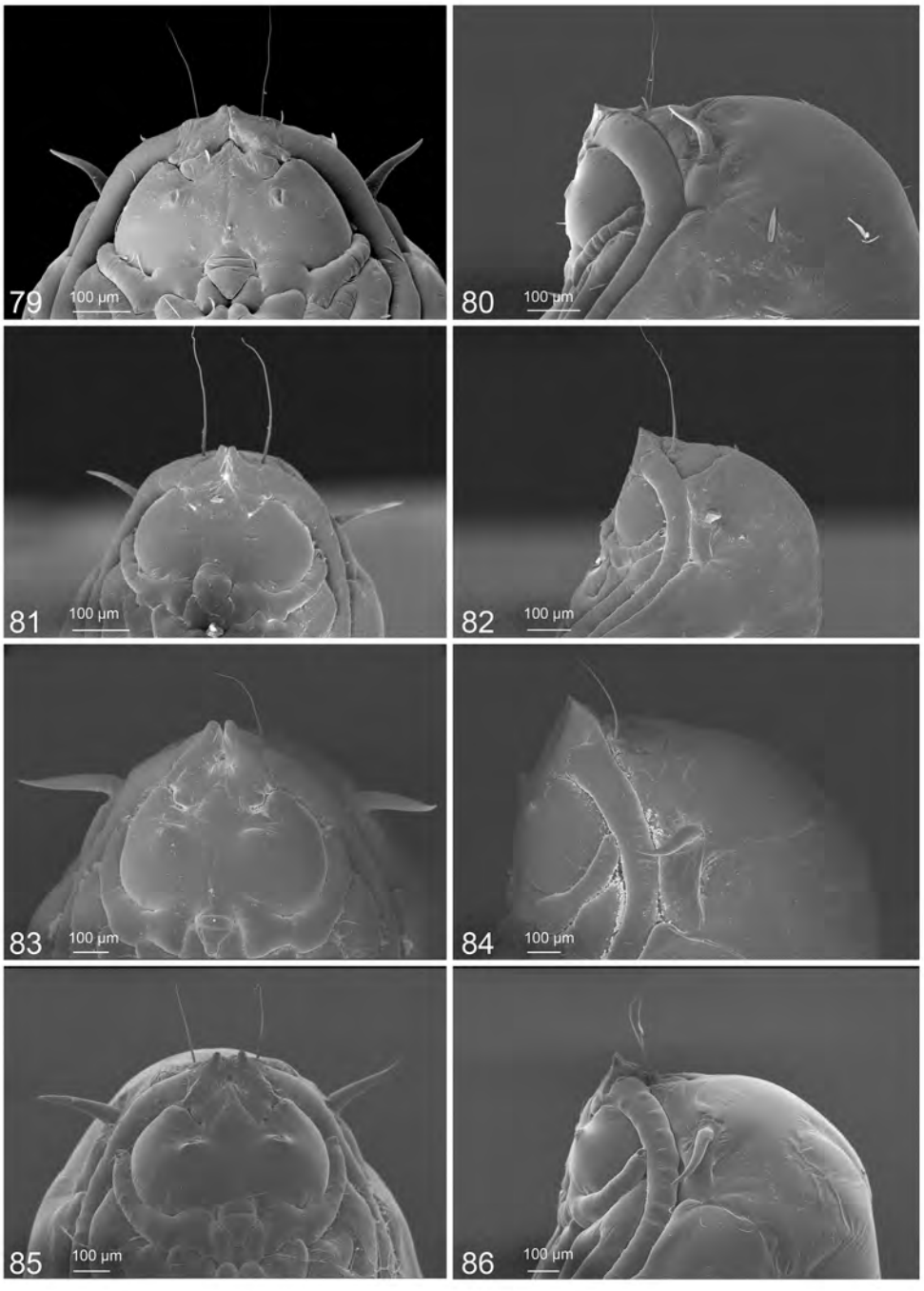
Figs. 55–62, *Celticecis* spp. 55, *C. connata*, male head, frontal. 56, *C. aciculata*, female head, lateral. 57, *C. connata*, end of fifth tarsomere, lateral. 58–60, *C. celtiphyllia*, male terminalia: 58, Dorsal. 59, Dorsocaudal. 60, Ventral. 61, *C. connata*, male terminalia, dorsal. 62, *C. japonica*, female eighth segment through cerci, lateral.



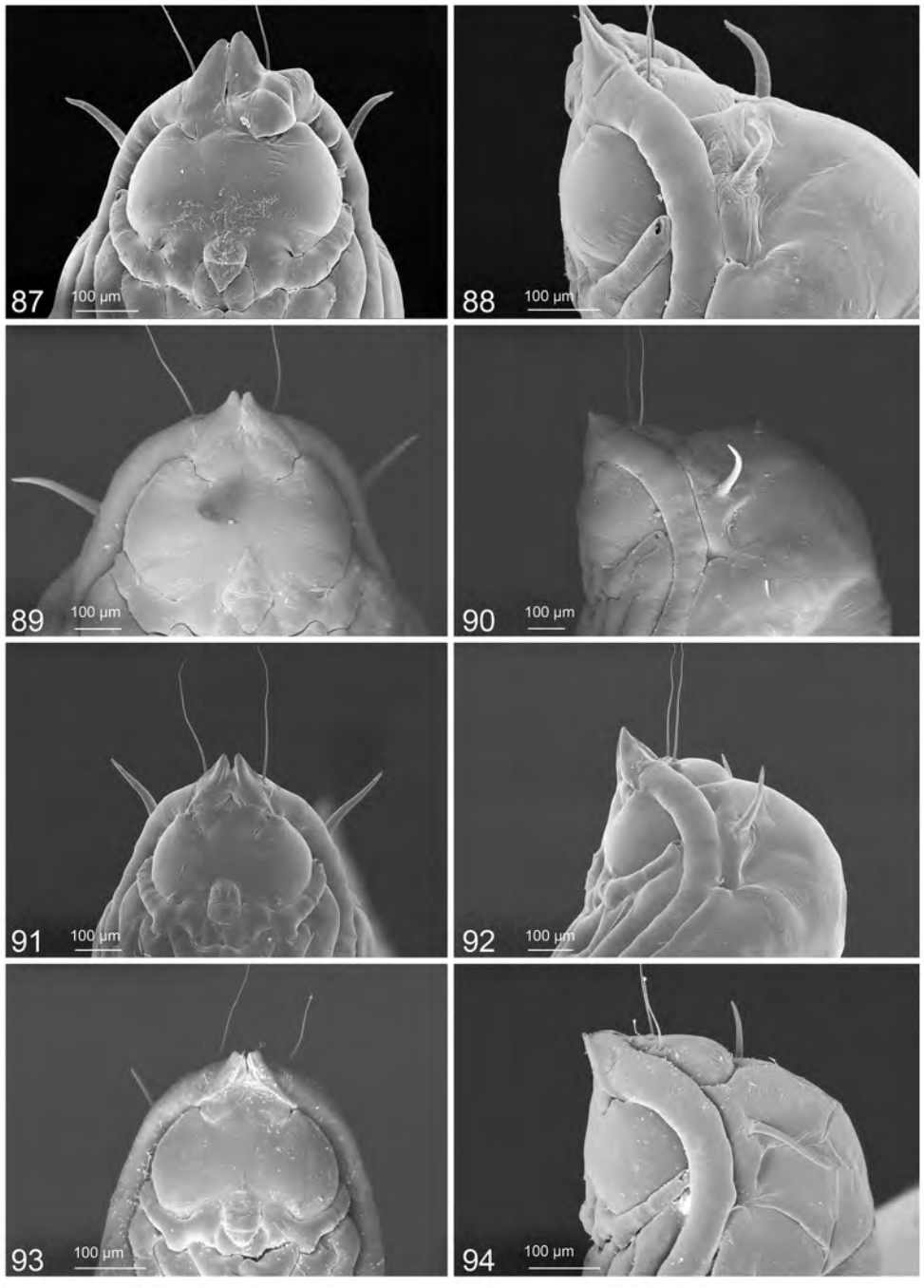
Figs. 63–70, *Celticecis* spp. 63–65, *C. japonica*, female eighth segment through cerci: 63, Lateral. 64, Dorsal; 65,caudal. 66–68, *C. celtiphyllia*: 66 Postabdomen, lateral. 67, Cerci and hypoproct, lateral. 68, Same, dorsal. 69–70, *C. spiniformis*: 69, Eighth segment through cerci, dorsal. 70, Postabdomen, lateral.



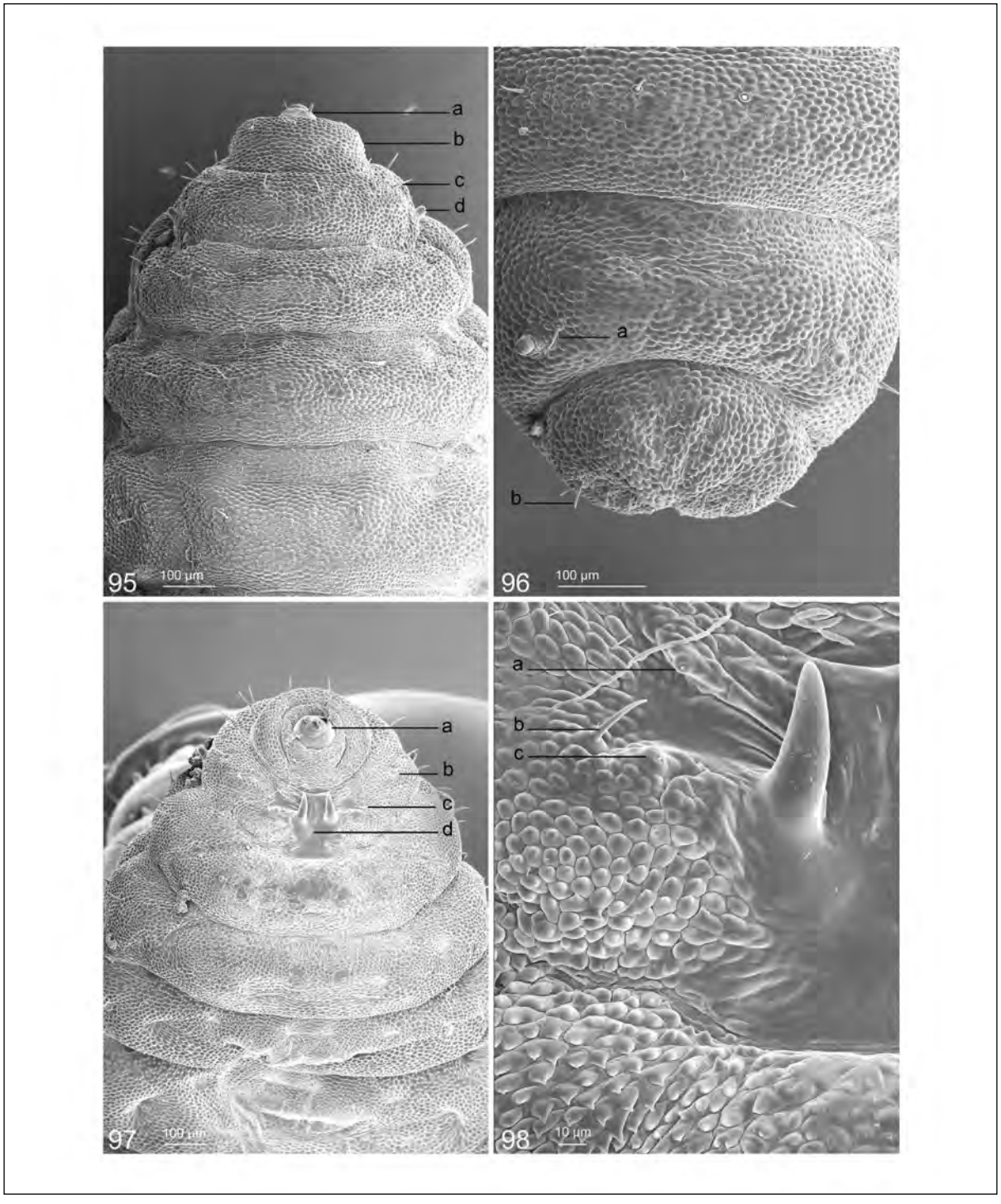
Figs. 71–78. Pupae of *Celticecis* spp. 71–72, *C. celtiphyllia*: 71, Ventral. 72, Dorsal. 73–78, Anterior segments, ventral and lateral. 73–74, *C. celtiphyllia*. 75–76, *C. aciculata*. 77–78, *C. acuminata*.



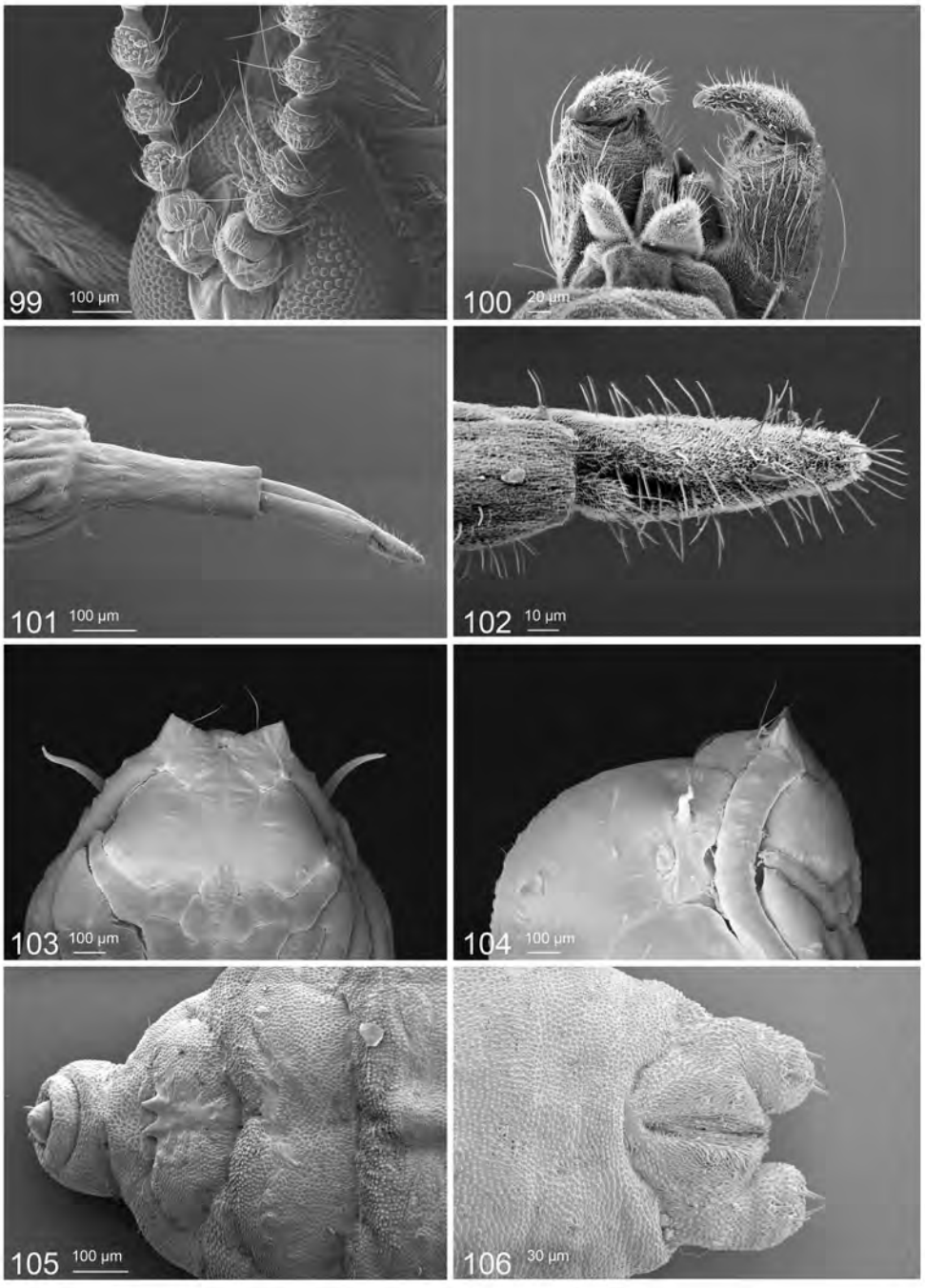
Figs. 79–86. Pupae of *Celticecis* spp., anterior segments, ventral and lateral. 79–80, *C. capsularis*. 81–82, *C. conica*. 83–84, *C. connata*. 85–86, *C. expulsa*.



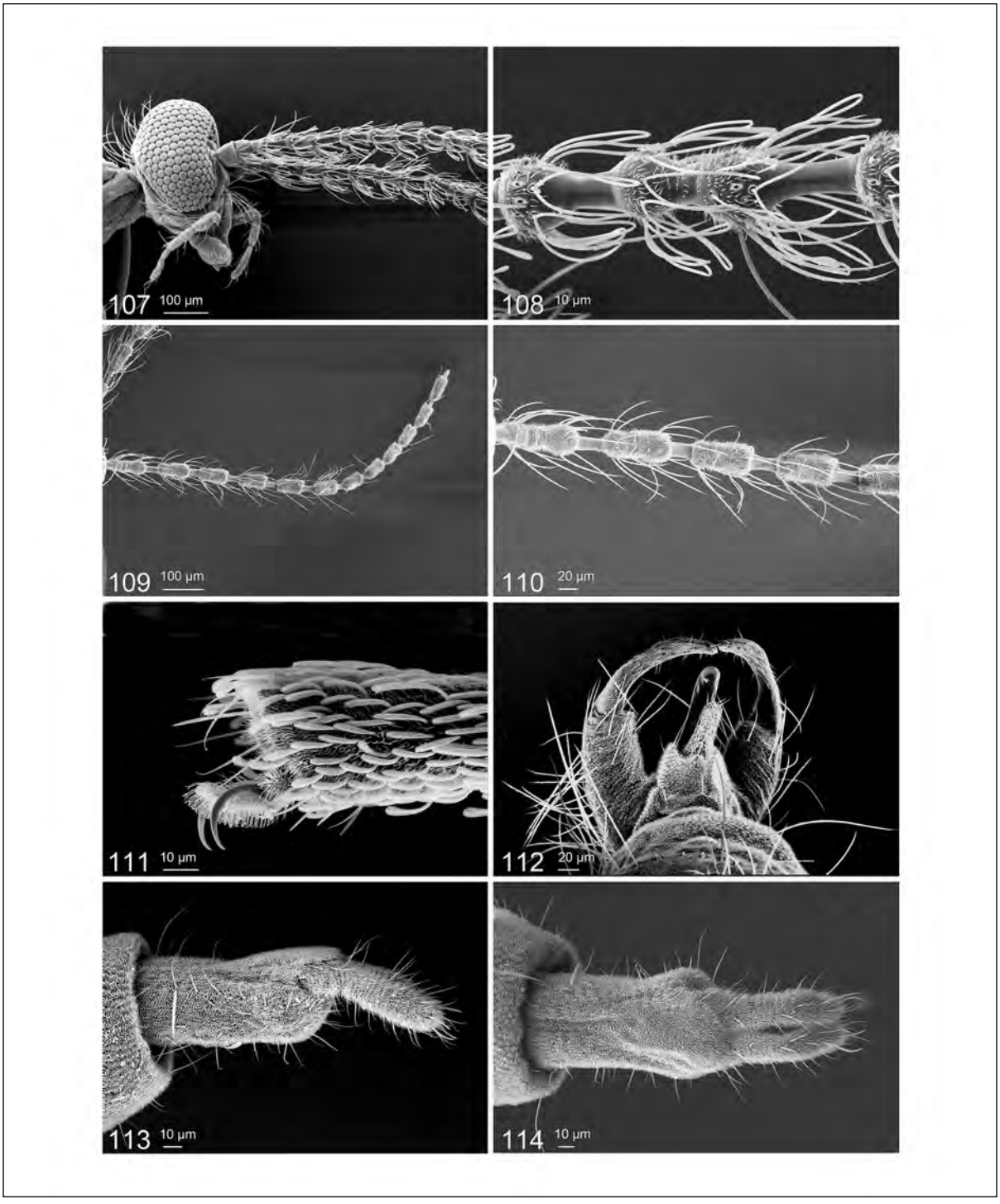
Figs. 87–94. Pupae of *Celticecis* spp., anterior segments, ventral and lateral. 87–88, *C. globosa*, one antenna deformed. 89–90, *C. pubescens*. 91–92, *C. spiniformis*. 93–94, *C. supina*.



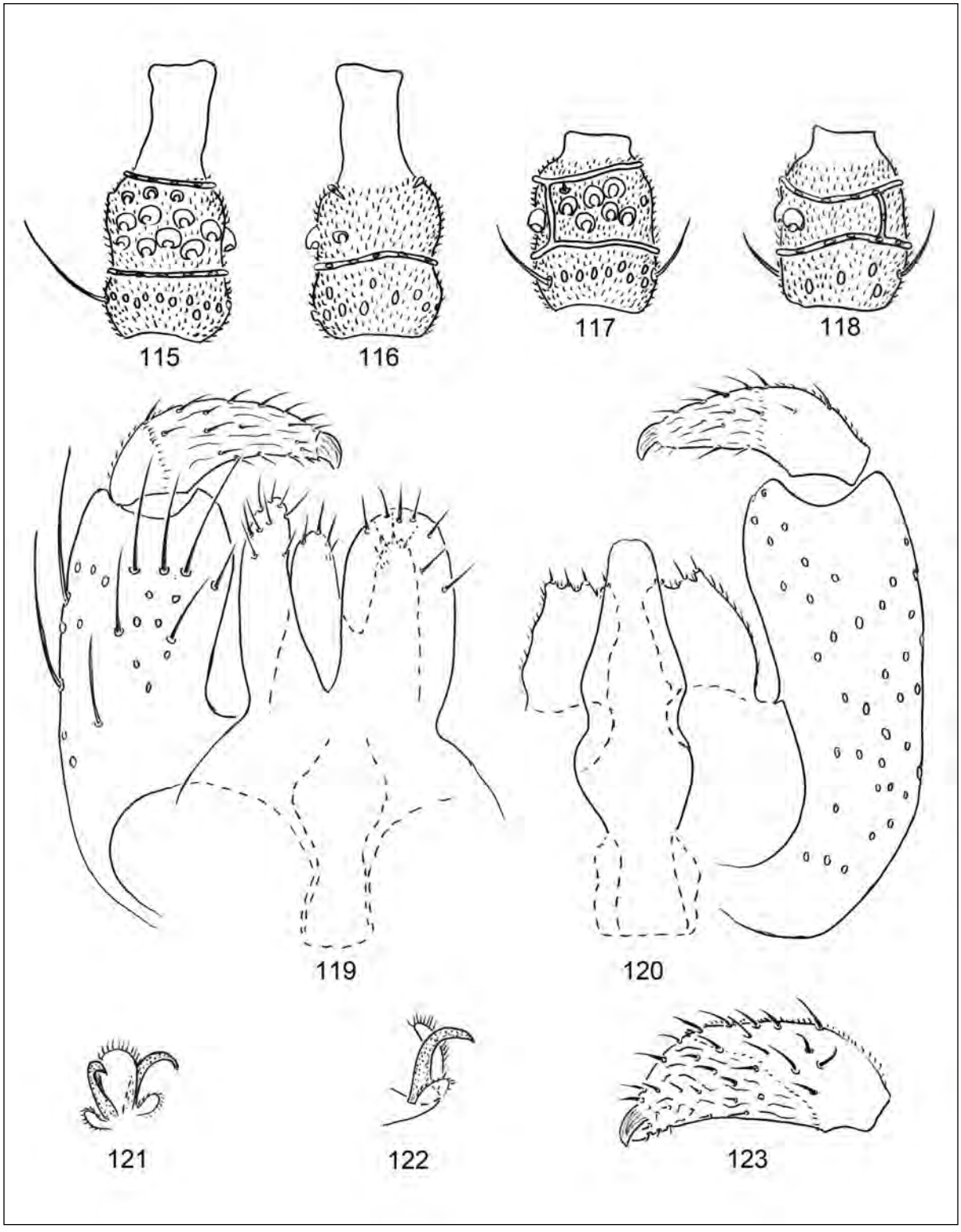
Figs. 95–98, *Celticecis celtiphyllia*, larvae. 95, Anterior segments, dorsal: a = head; b = collar segment; c = dorsal papillae; d = spiracle. 96, Posterior segments, dorsal: a = dorsal papilla; b = terminal papilla. 97, Anterior segments, ventral: a = head; b = pleural papilla; c = ventral papilla; d = spatula. 98, Detail of part of spatula and surrounding area: a = sternal papilla; b = ventral papilla; c = lateral papillae.



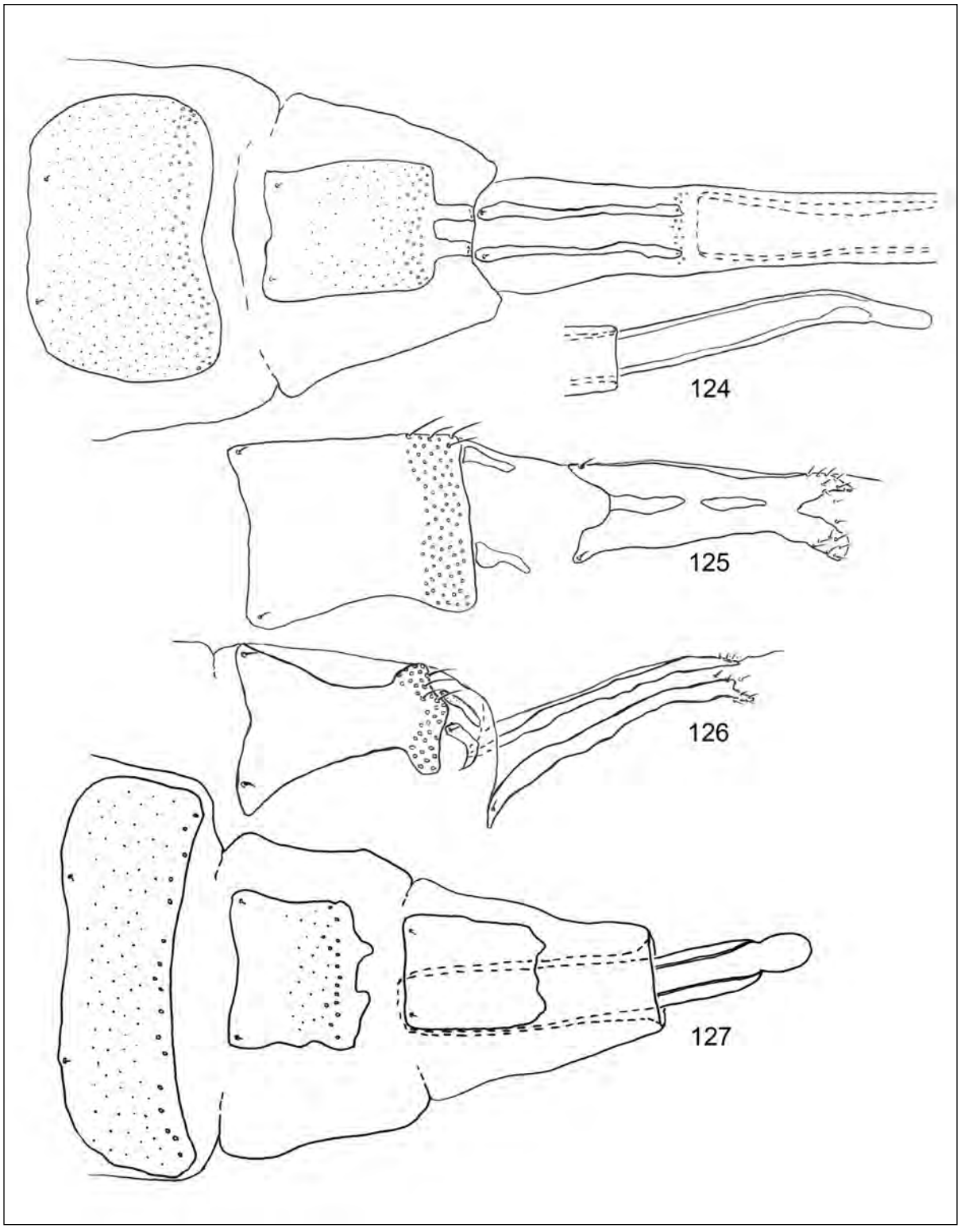
Figs. 99–106. *Peracecis fugitiva*. 99, Male antennal bases, ventral. 100, Male terminalia, dorsal. 101, Female postabdomen, lateral. 102, Female fused cerci and hypoproct, lateroventral. 103, Pupal anterior segments, ventral. 104, Same, lateral. 105, Third instar larva, anterior segments, ventral. 106, Same, posterior segments, ventral.



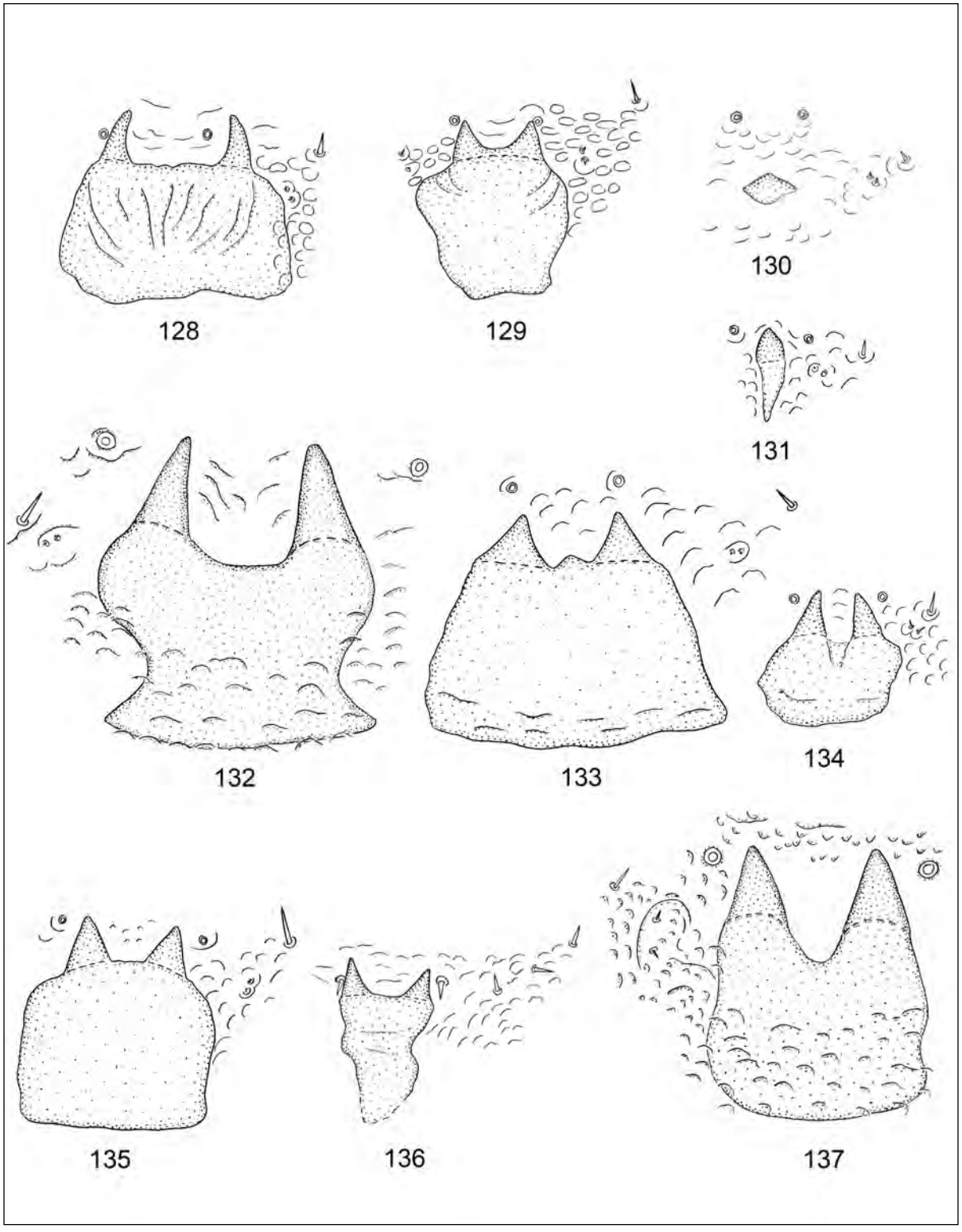
Figs. 107–114. *Parallelodiplosis acernea*. 107, Male head, lateral. 108, Male third flagellomere, lateral. 109, Female flagellum, dorsal. 110, Same, basal four flagellomeres. 111, Fifth foretarsomere, lateral. 112, Male terminalia, dorsal. 113, Female postabdomen, lateral. 114, Same, dorsal.



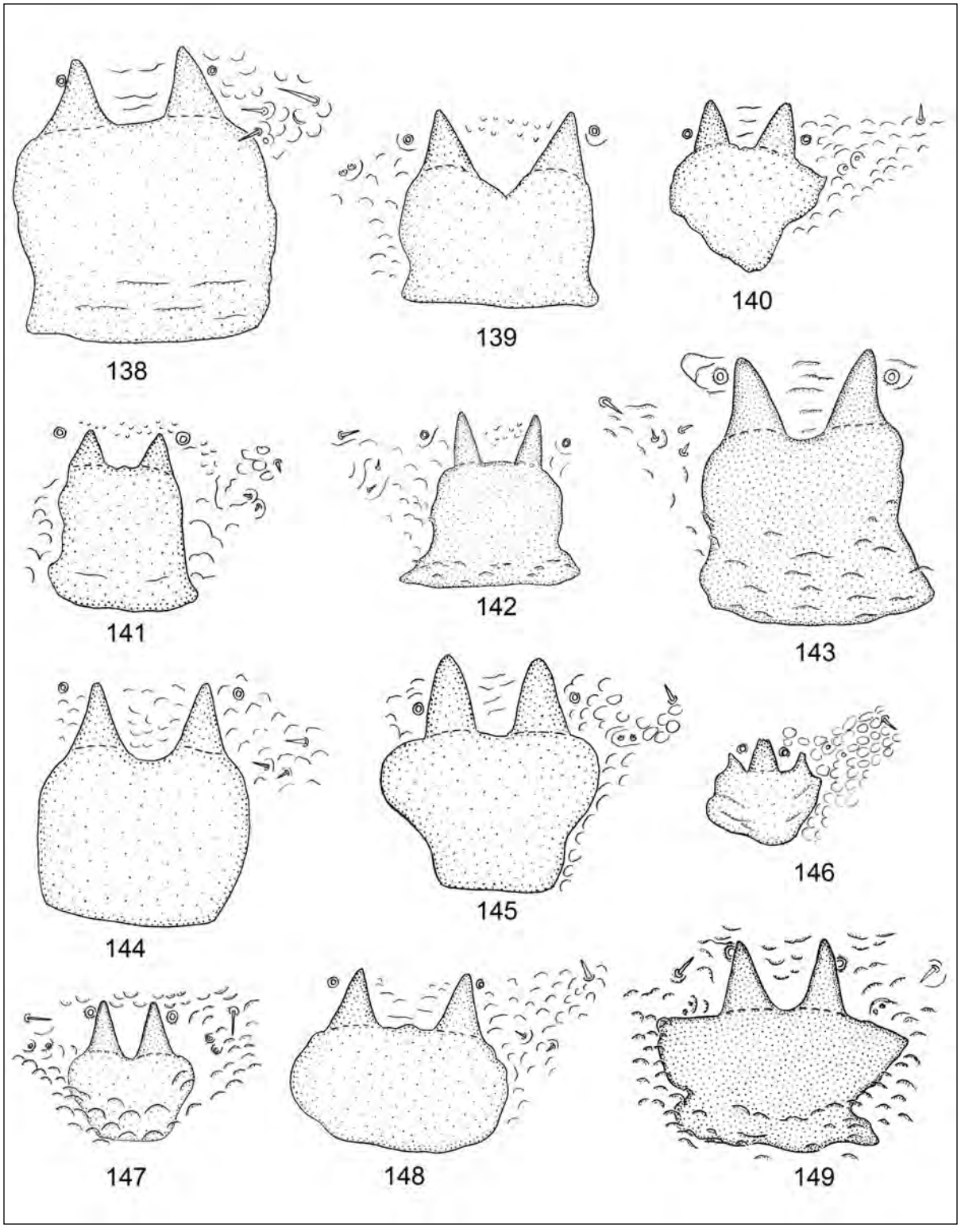
Figs. 115–123, *C. celtiphyllia*. 115, Male third flagellomere, ventral. 116, Same, dorsal. 117, Female third flagellomere, ventral. 118, Same, dorsal. 119, Male terminalia, right gonopod not shown, dorsal. 120, Same, ventral. 121, Acropod, ventrolateral. 122, Same, lateral. 123, *C. expulsa*, gonostylus, dorsal.



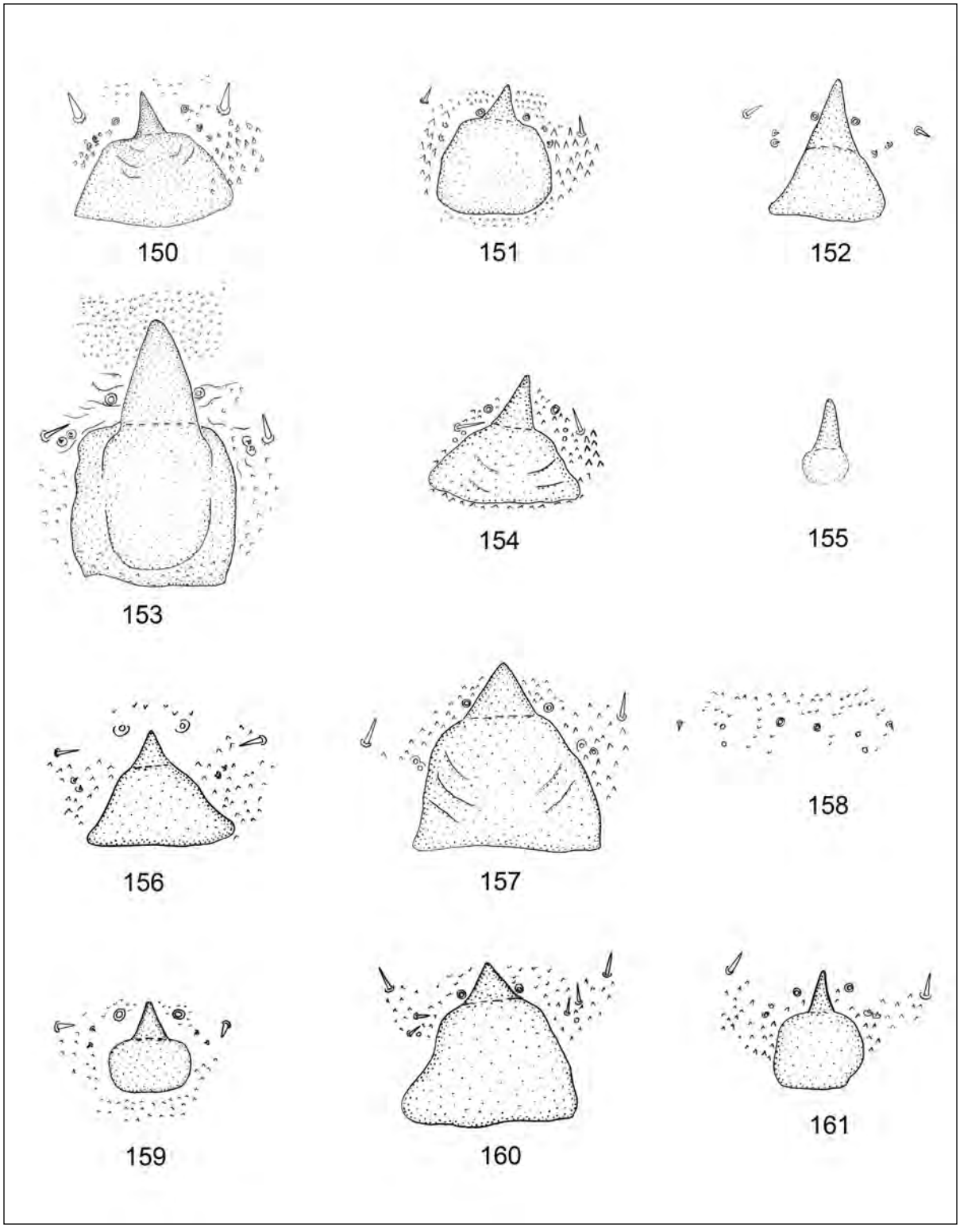
Figs. 124–127, *Celticecis spp*., female postabdomens, dorsal. 124, *C. celtiphyllia*, sixth tergite through fused cerci. 125, *C. connata*, seventh and eighth tergites. 126, *C. expulsa*, seventh and eighth tergites. 127, *C. conica*, sixth tergite through cerci.



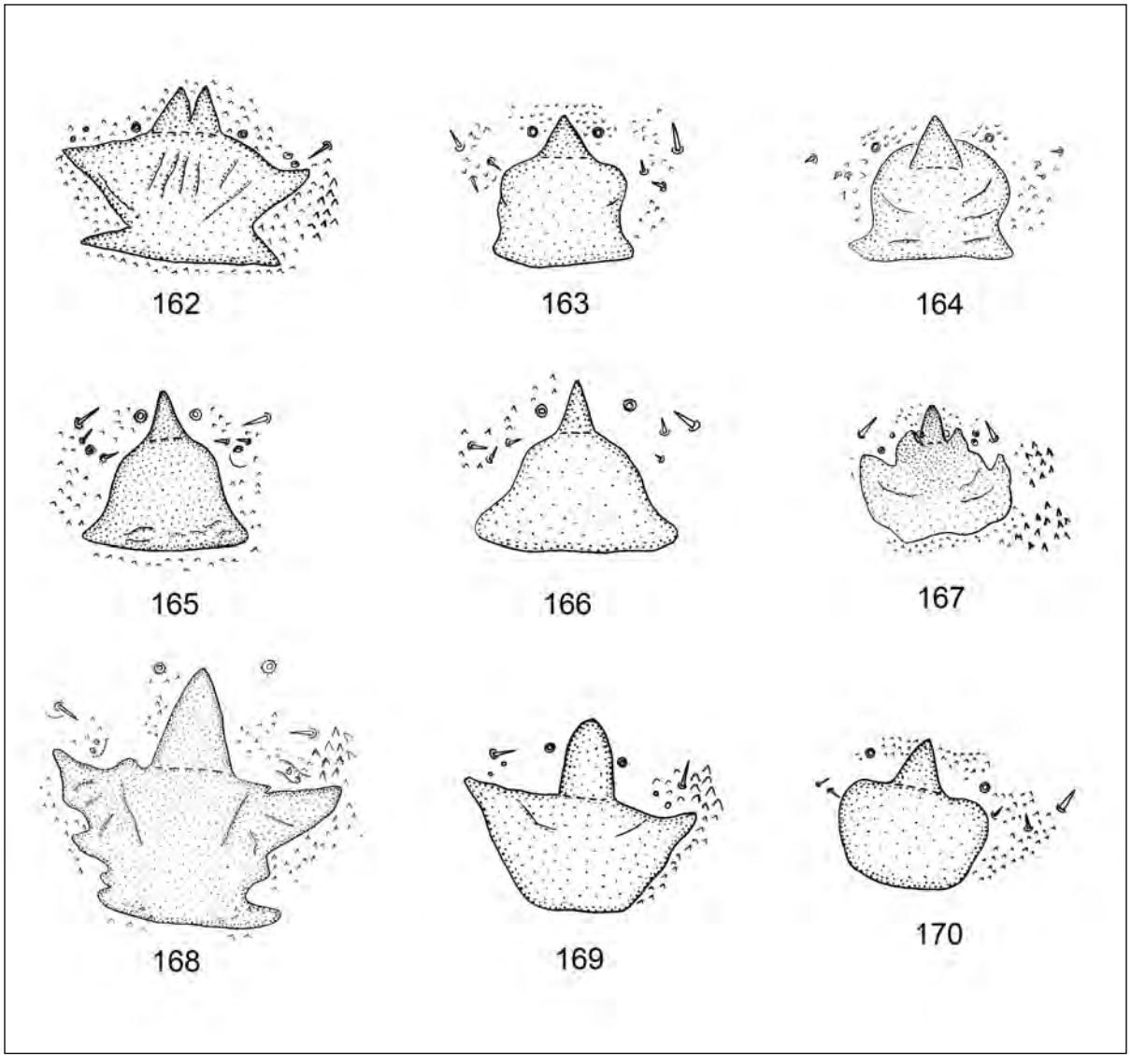
Figs. 128–137. Third instar spatulas and adjacent papillae of *Celticecis* spp., all to same scale. 128, *C. aciculata*. 129, *C. acuminata*. 130, *C. capsularis*. 131, *C. cupiformis*. 132, *C. celtiphyllia*. 133, *C. expulsa*. 134, *C. conica*. 135, *C. connata*. 136, *C. cornuata*, 137, *C. globosa*.



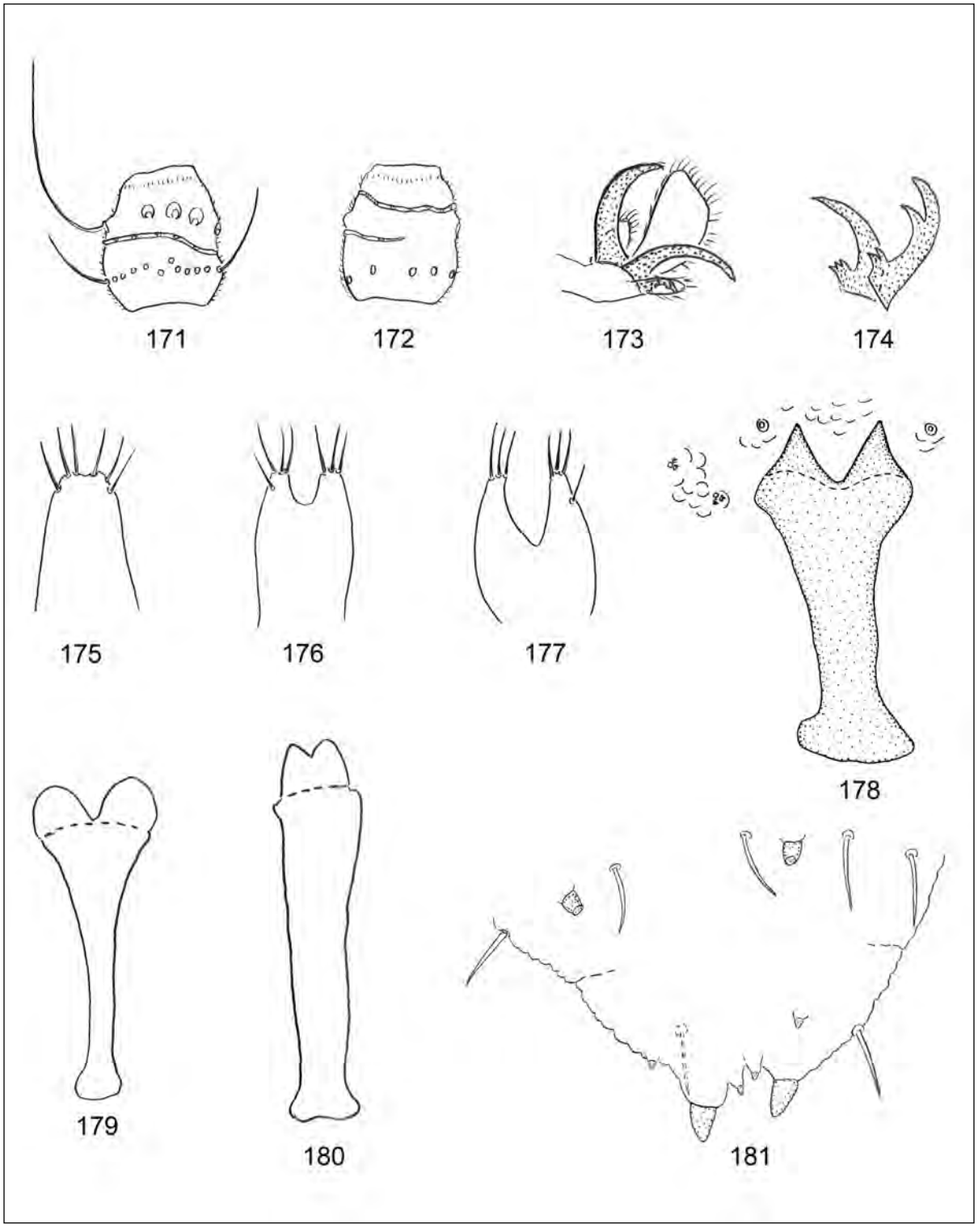
Figs. 138–149. Third instar spatulas and adjacent papillae of *Celticecis* spp., all to same scale. 138, *C. ovata*. 139, *C. oviformis*. 140, *C. pilosa*. 141, *C. pubescens*. 142, *C. pyriformis*. 143, *C. ramicola*. 144, *C. semenrumicis*. 145, *C. spiniformis*. 146, *C. spiniformis*, "Ithaca type." 147, *C. supina*. 148, *C. subulata*. 149, *C. wellsi*.



Figs. 150–161. Second instar spatulas and adjacent papillae of *Celticecis* spp., all to same scale.150, *C. aciculata*. 151, *C. acuminata*. 152, *C. capsularis*. 153, *C. celtiphyllia*. 154, *C. conica*. 155, *C. cupiformis*. 156, *C. expulsa*. 157, *C. connata*. 158, *C. cornuata* (spatula not present). 159, *C. globosa*. 160, *C. ovata*. 161, *C. oviformis*.



Figs. 162–170. Second instar spatulas and adjacent papillae of *Celticecis* spp., all to same scale.162, *C. pilosa*. 163, *C. pubescens*. 164, *C. pyriformis*. 165, *C. ramicola*. 166, *C. semenrumicis*. 167, *C. spiniformis*. 168, *C. subulata*. 169, *C. supina*. 170, *C. wellsi*.



Figs. 171–181. Body parts of *Peracecis fugitiva* and *Parallelodiplosis* spp. 171–178, *Peracecis fugitiva:* 171, Female third flagellomere, dorsal. 172, Same, ventral. 173, Acromere. 174, Pair of tarsal claws. 175–177, Male hypoproct, 3 examples, dorsal. 178, Larval spatula with sternal and lateral papillae. 179–181, *Parallelodiplosis* spp.: 179, Larval spatula, *P. acernea*. 180, Same, *P. caryae*. 181, Larval eighth and terminal abdominal segments, *P. acernea*, dorsal.

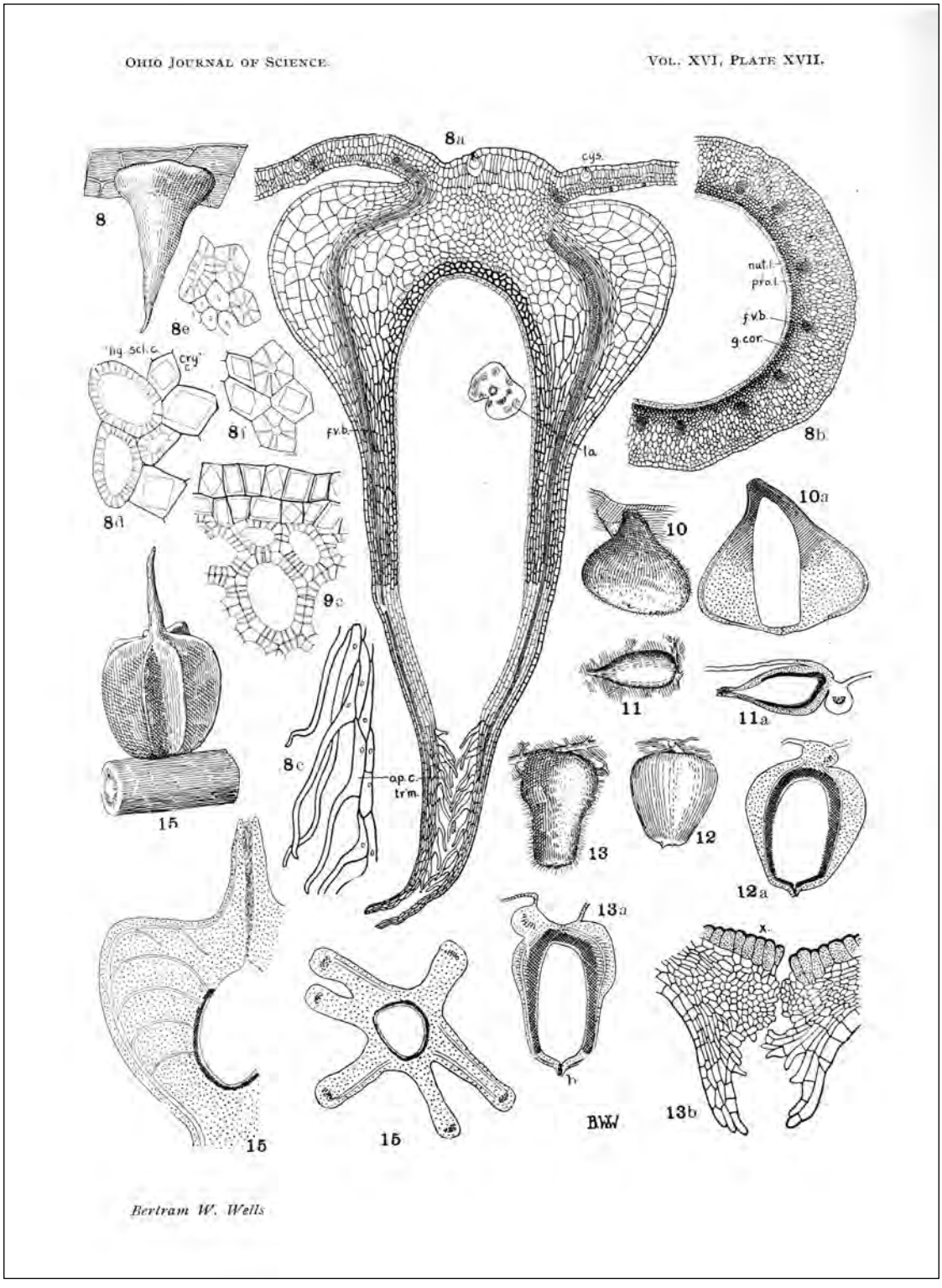


Plate 1. Galls of *Celticecis* spp., entire and in section, some with additional details. Figs. 8, 8a–f, *C. spiniformis*. Fig. 9c, *C. celtiphyllia*, sclerenchyma cells. Figs. 10, 10a, *C. wellsi*. Figs. 11, 11a, *C. supina*. Figs. 12, 12a, *C. globosa*. Figs. 13, 13 a–b, *C. pyriformis*. Fig. 15 (3 illus.), *C. semenrumicis*. Plate XVII of Wells (1916), reprinted through the courtesy of *The Ohio Journal of Science*.

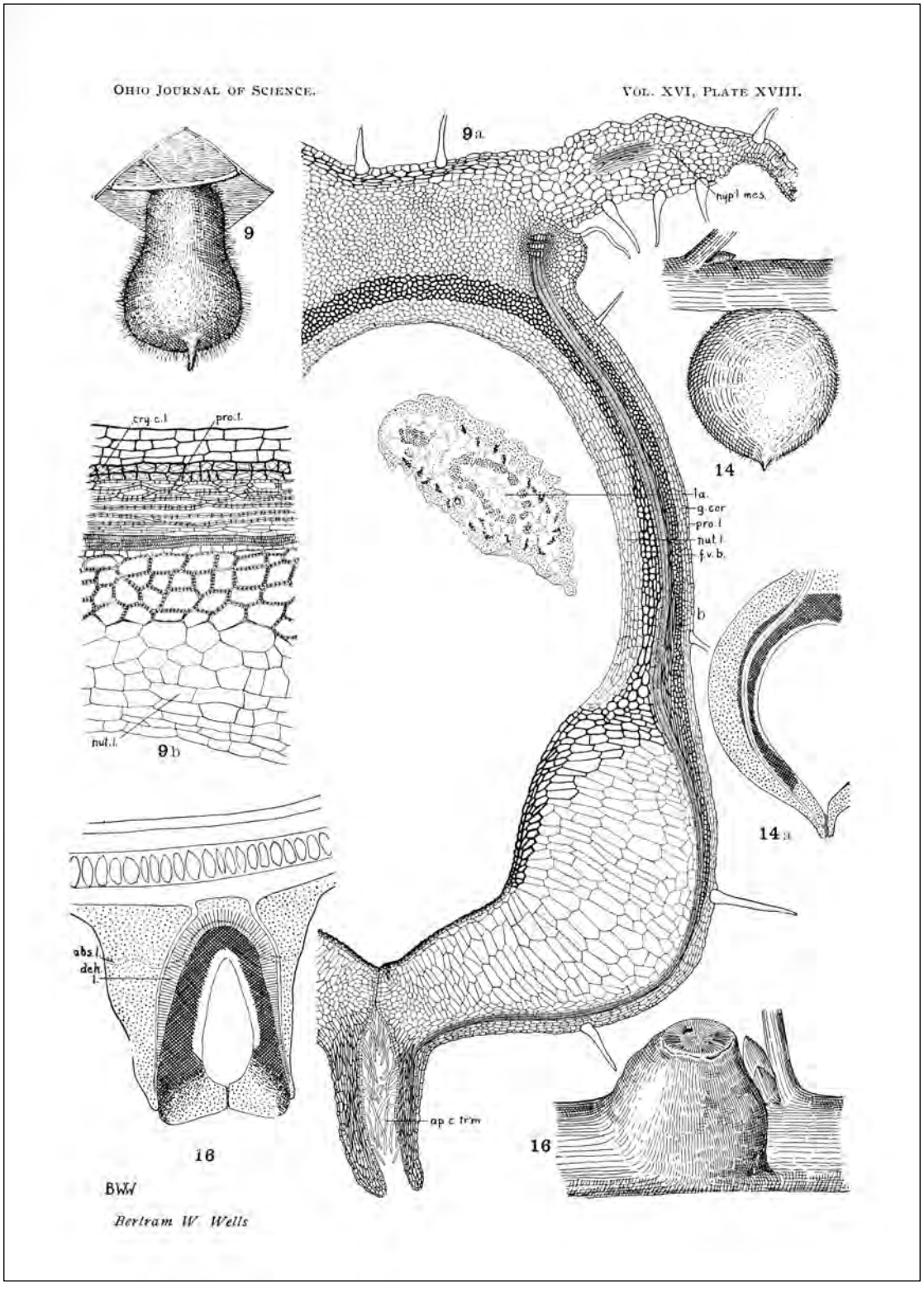
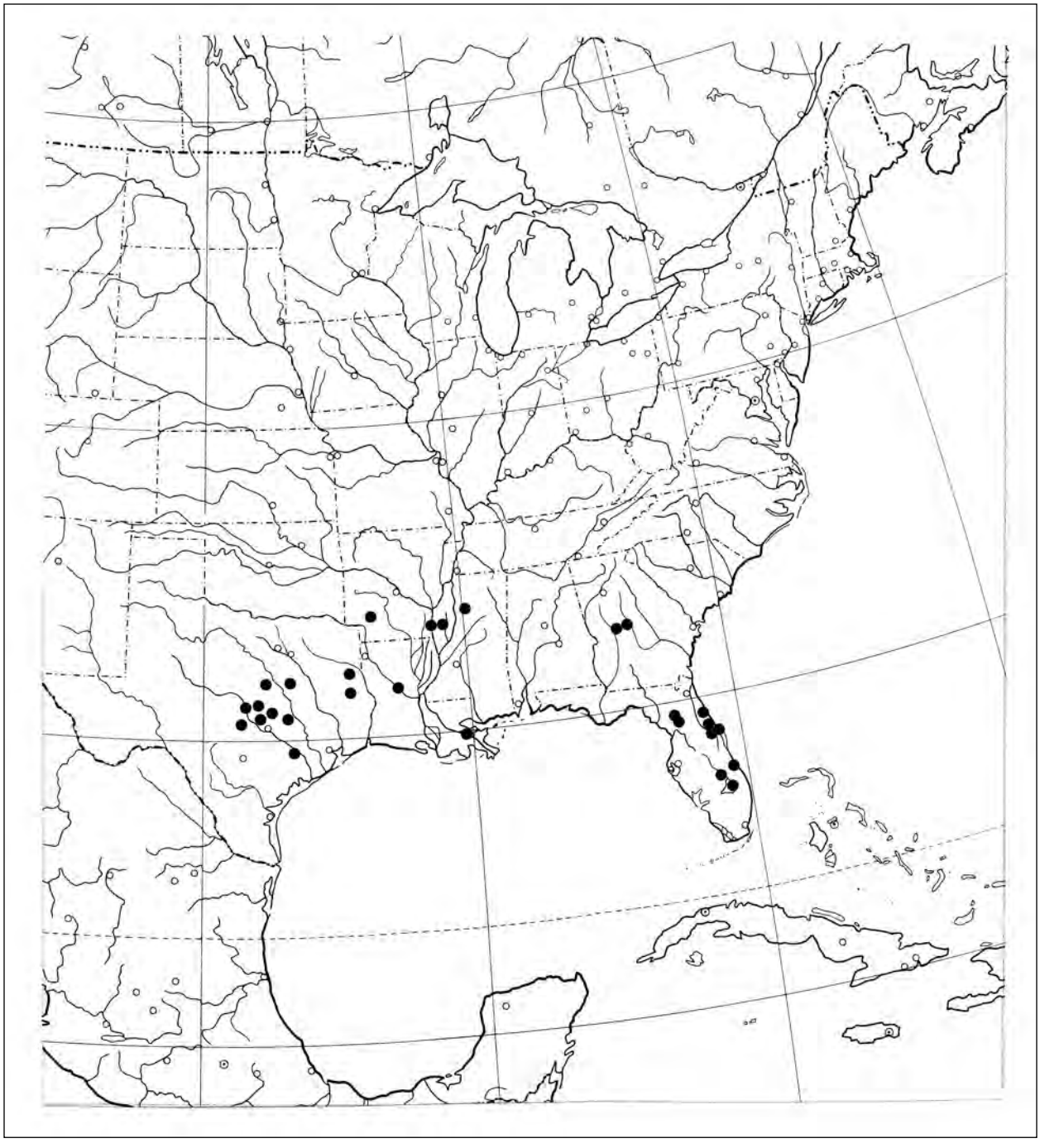
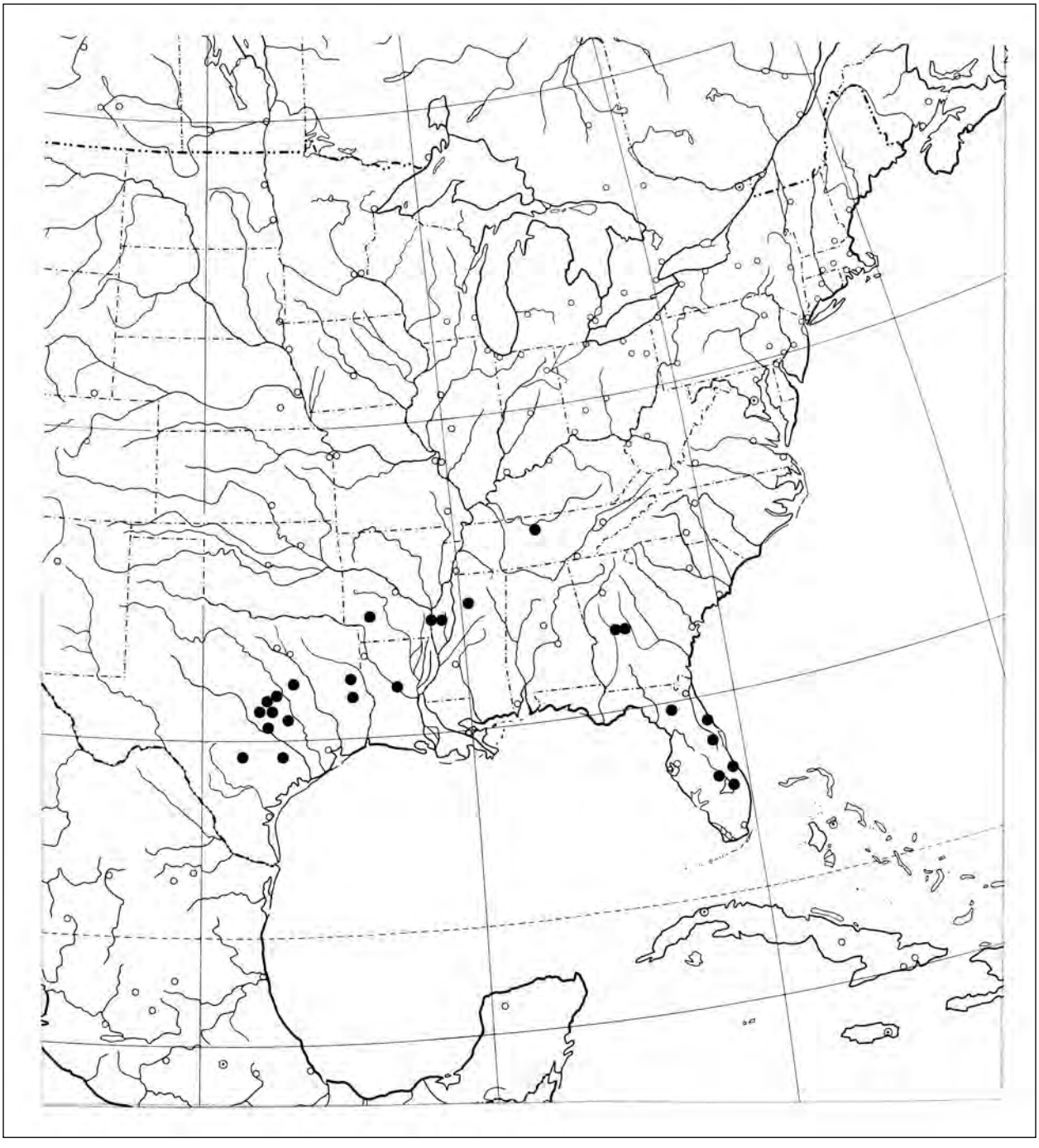


Plate 2. Galls of *Celticecis* spp., entire and in section, some with additional details. Figs. 9, 9a–b, *C. celtiphyllia*. Figs. 14, 14a, *C. oviformis*. Fig. 16 (2 illus.), *C. expulsa*. Plate XVIII of Wells (1916), reprinted through the courtesy of *The Ohio Journal of Science*.

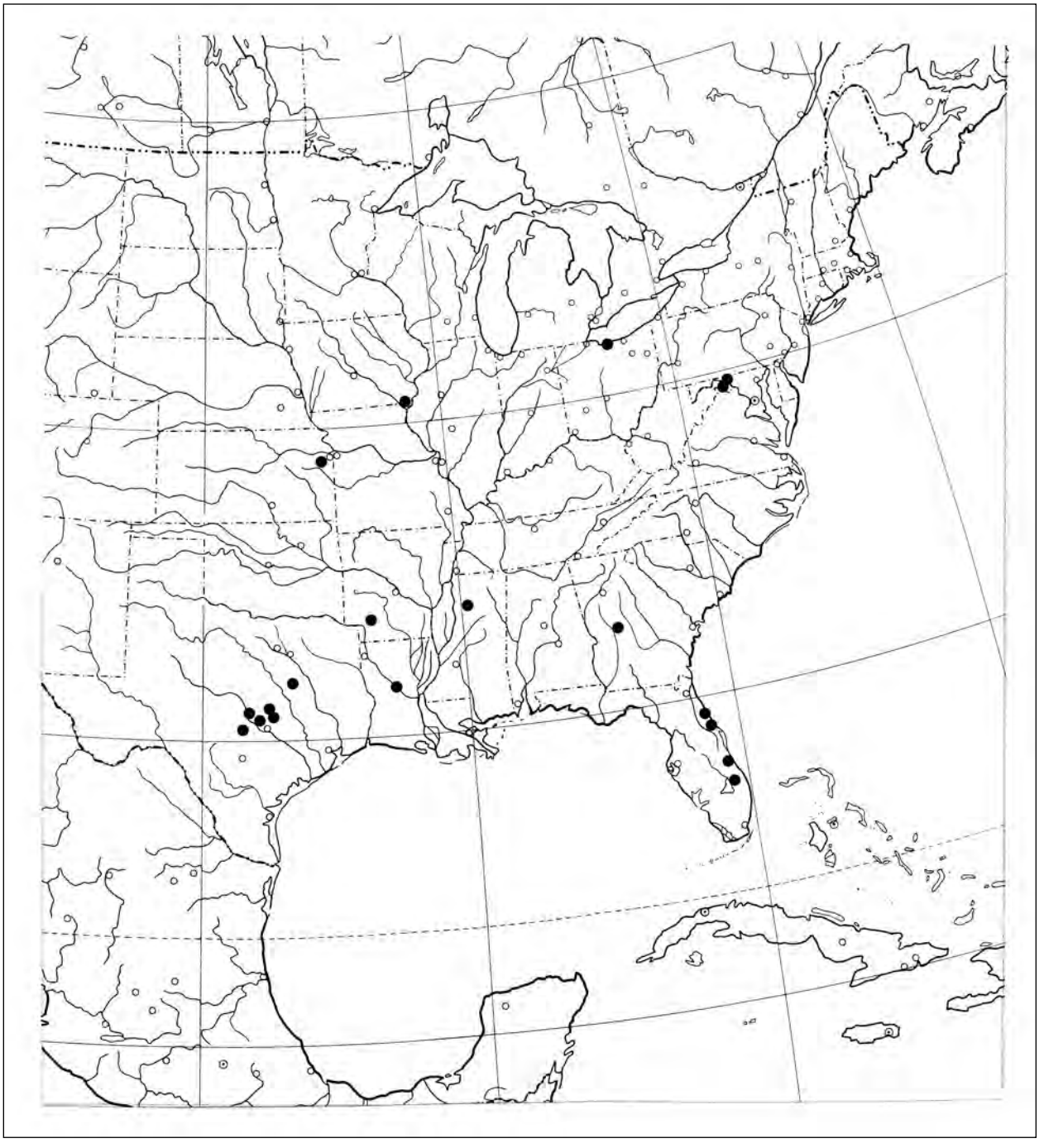


Map 1. Eastern North American distribution of *Celticecis aciculata*. It occurs also in Arizona.

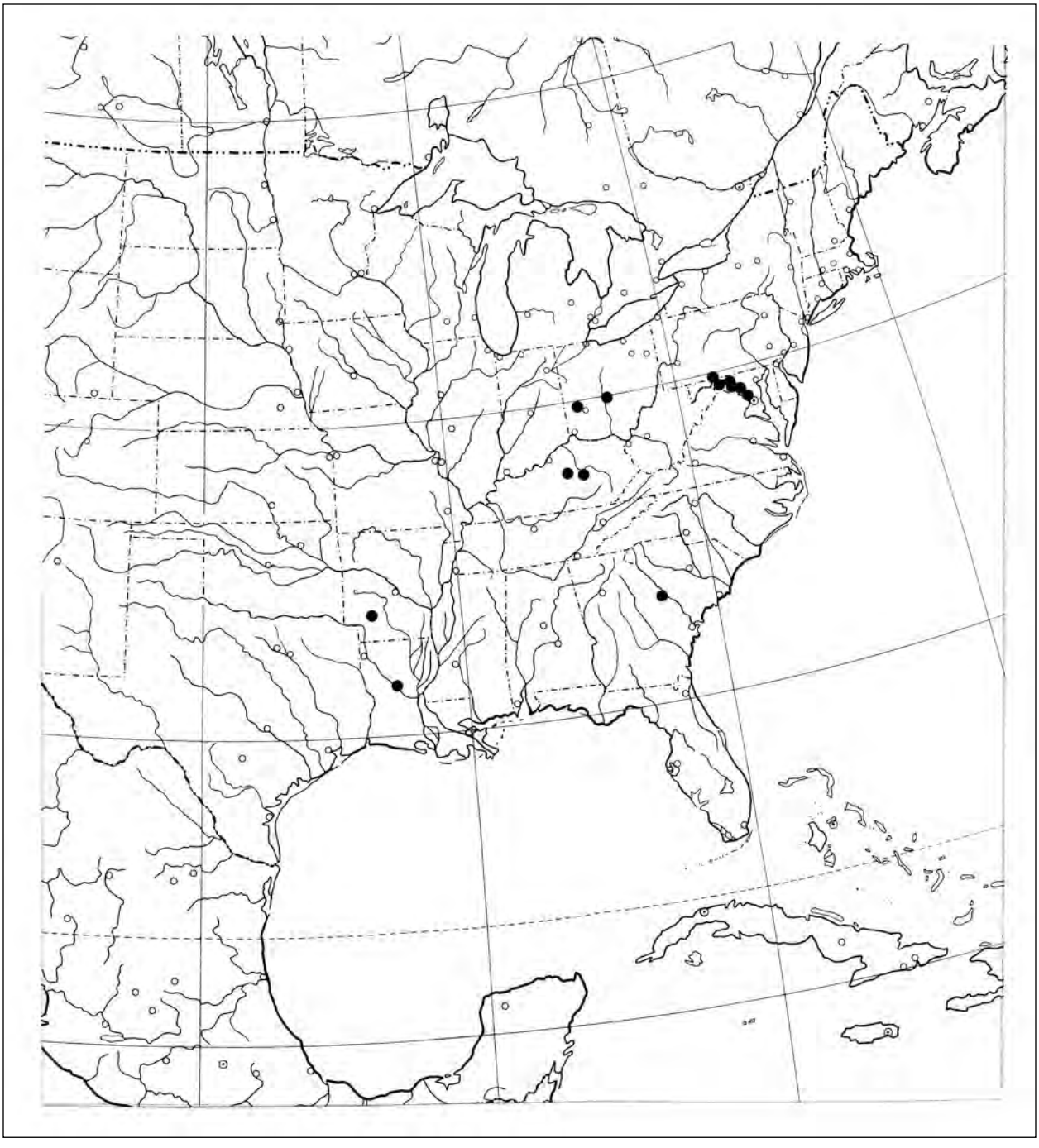
Map 2. Distribution of *Celticecis acuminata*.



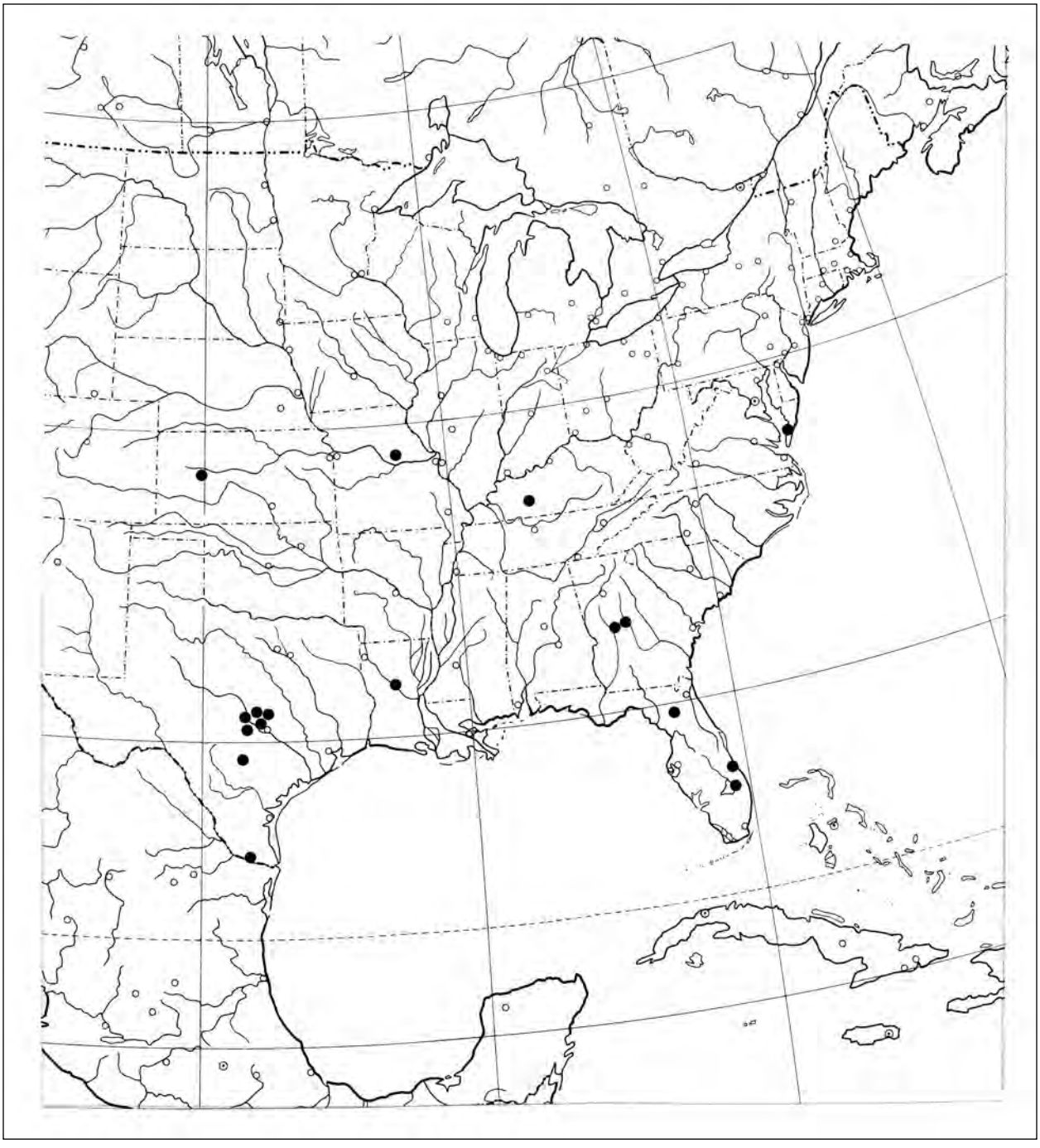
Map 3. Distribution of *Celticecis capsularis*.



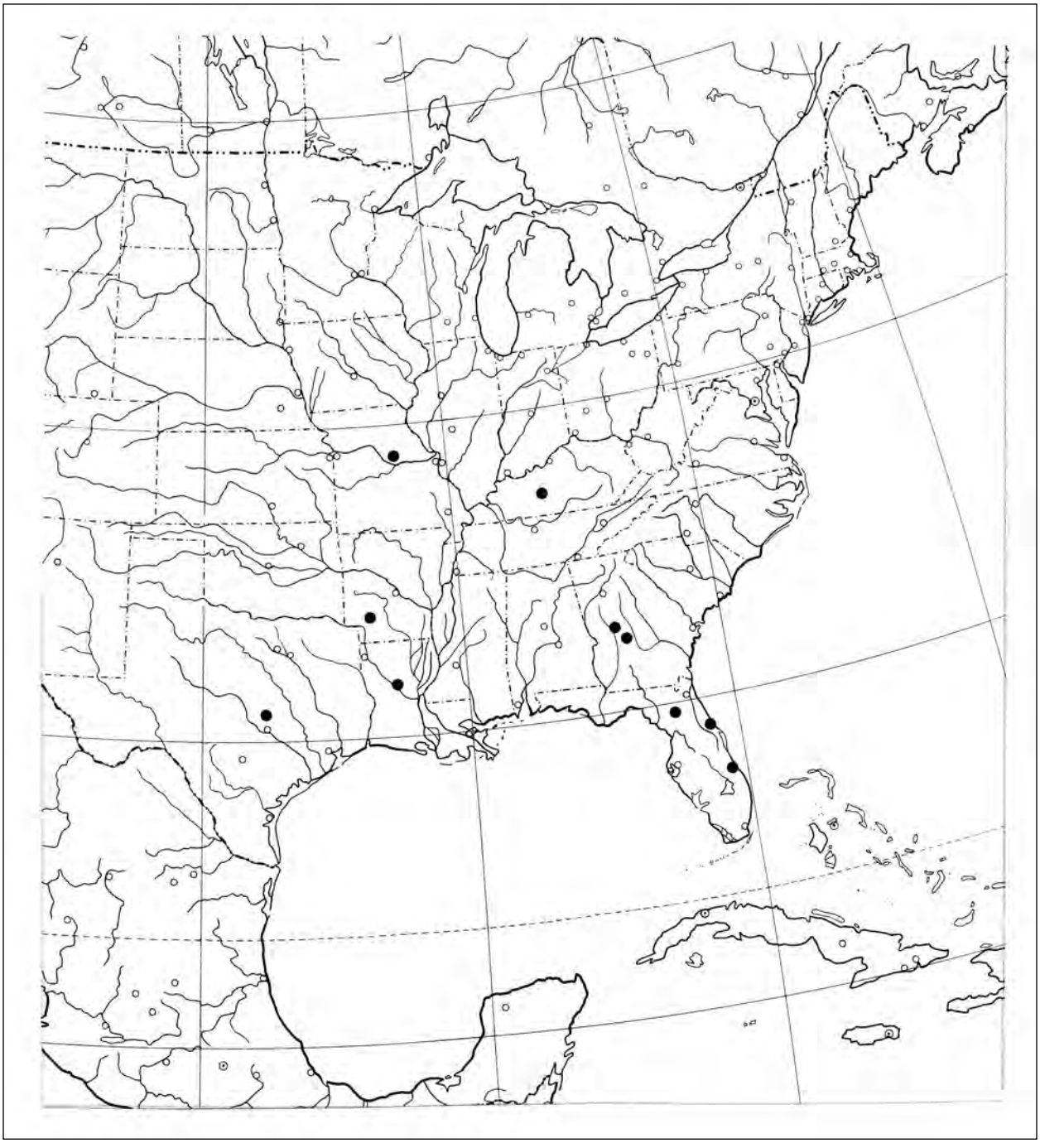
Map 4. Distribution of *Celticecis celtiphyllia*.



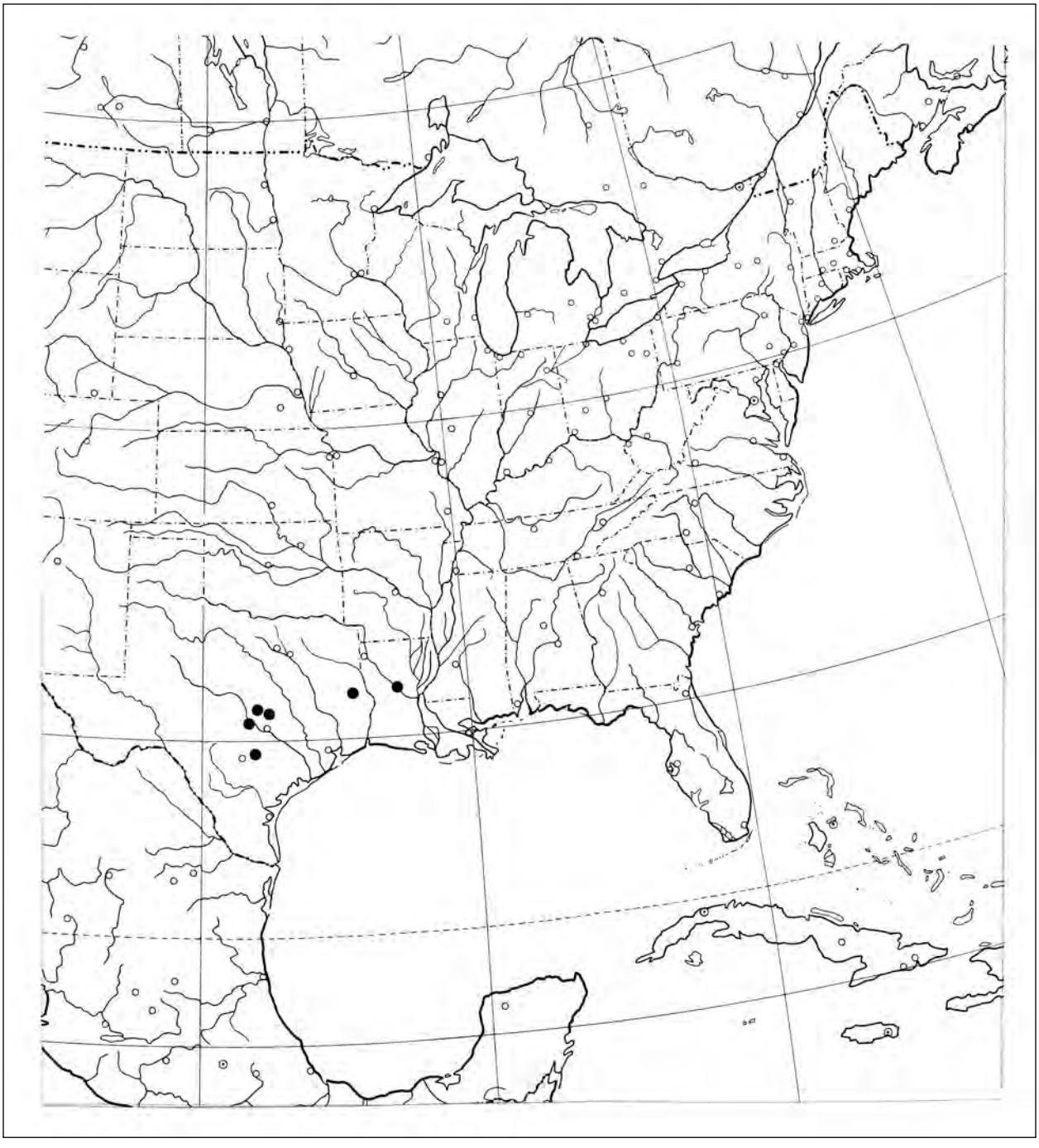
Map 5. Distribution of *Celticecis conica*.



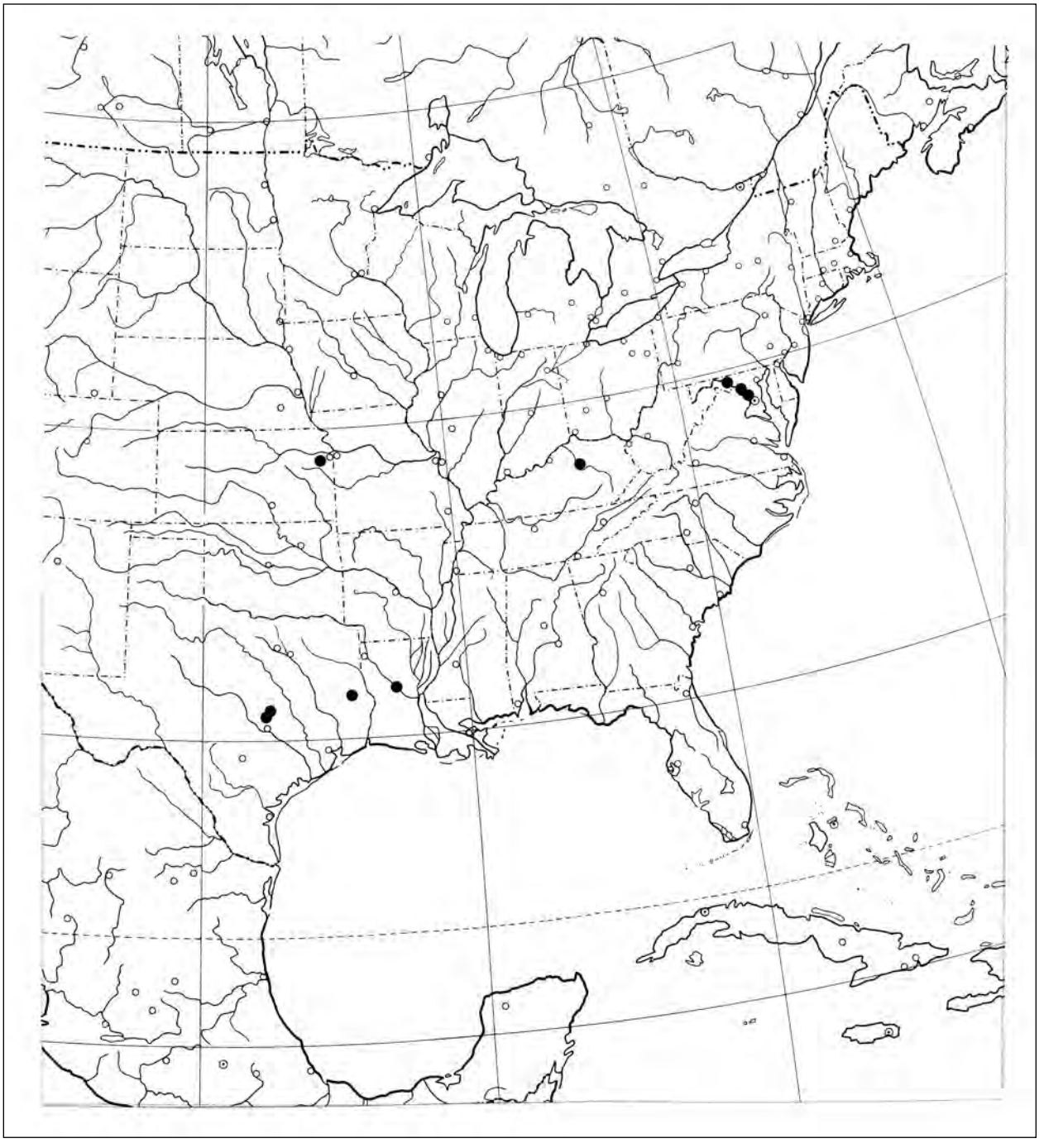
Map 6. Eastern North American distribution of *Celticecis connata*. It occurs also in Arizona.



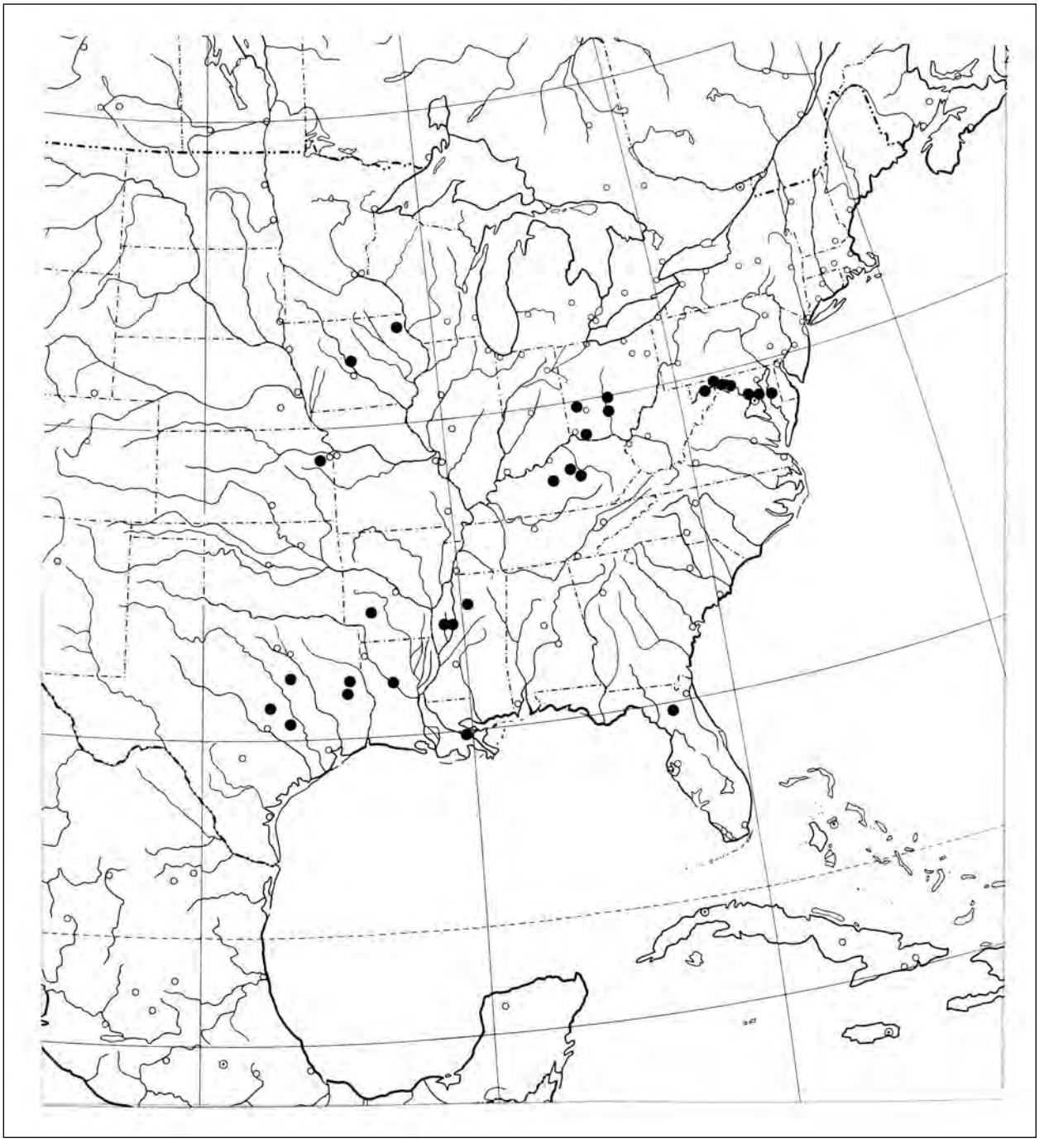
Map 7. Distribution of *Celticecis cornuata*.



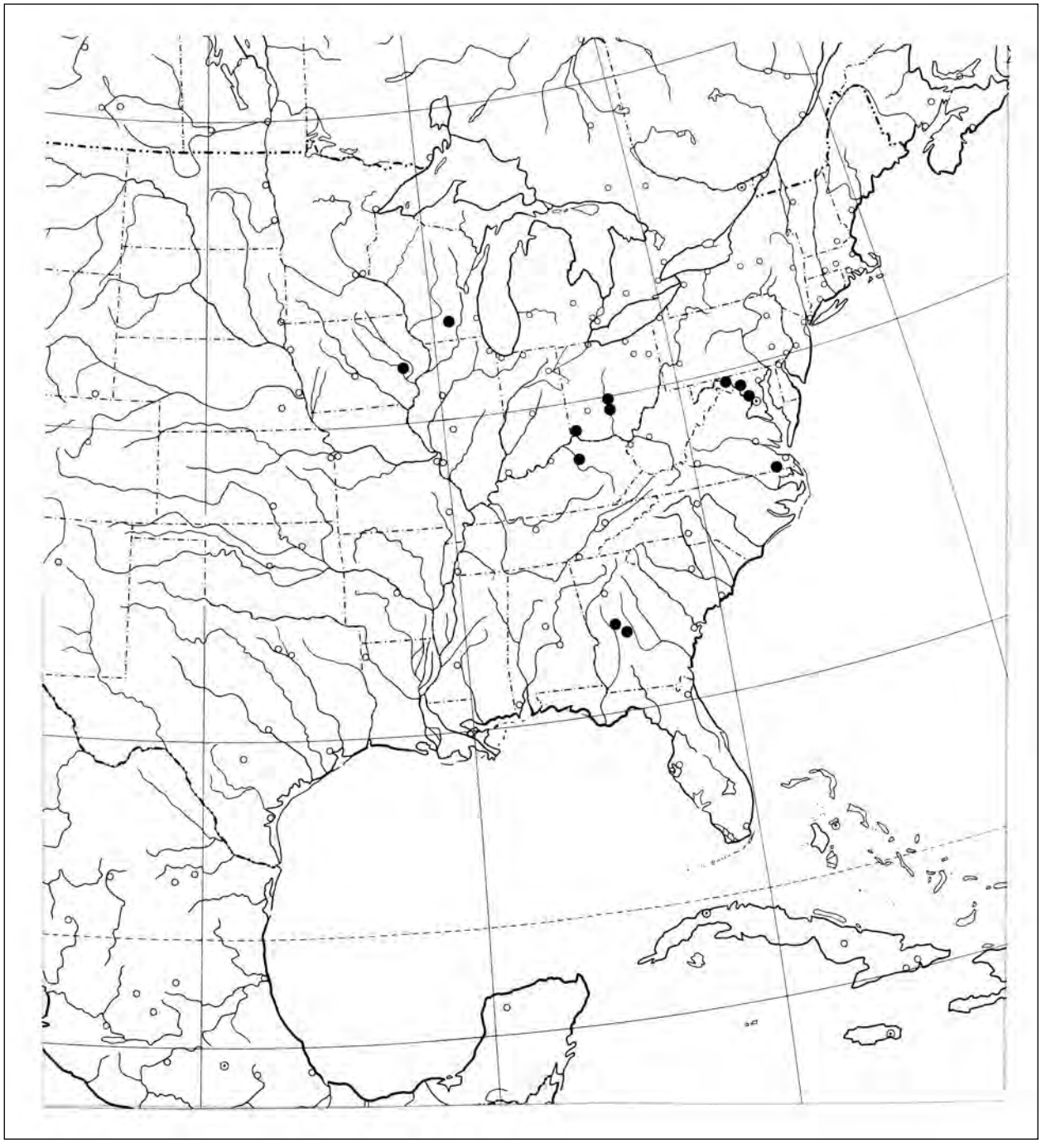
Map 8. Distribution of *Celticecis cupiformis*.



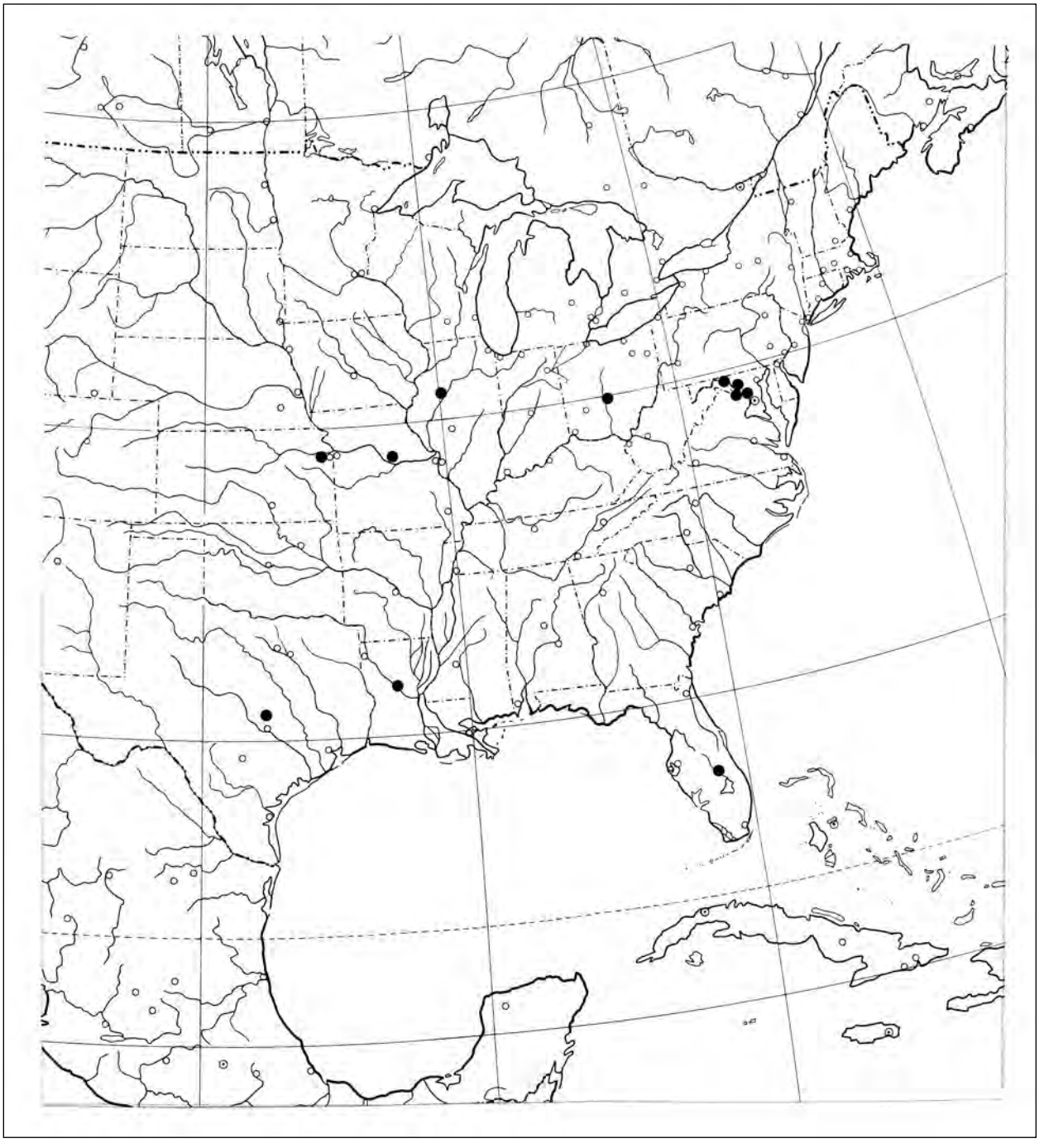
Map 9. Distribution of *Celticecis expulsa*.



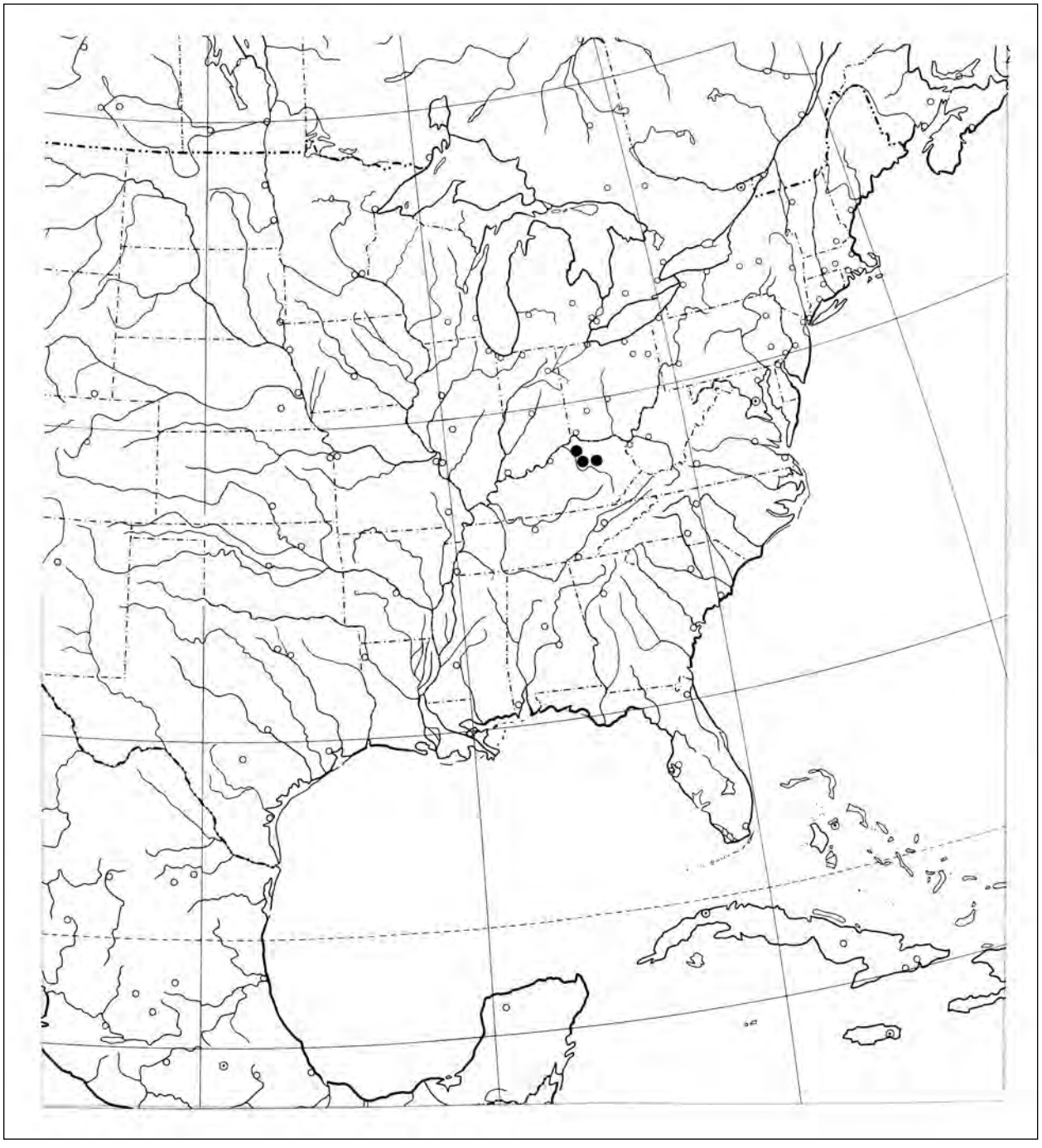
Map 10. Distribution of *Celticecis globosa*.



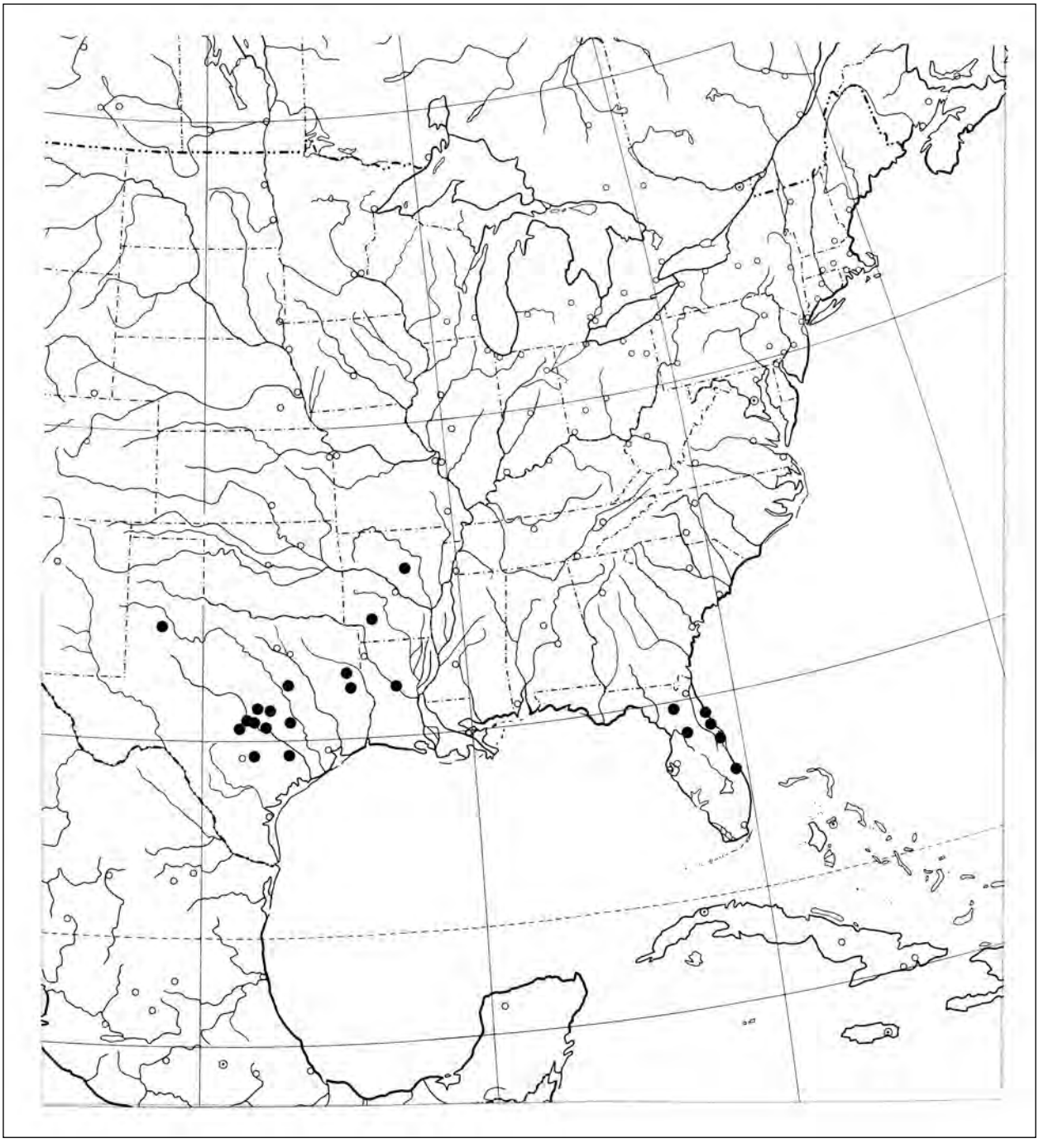
Map 11. Distribution of *Celticecis ovata*.



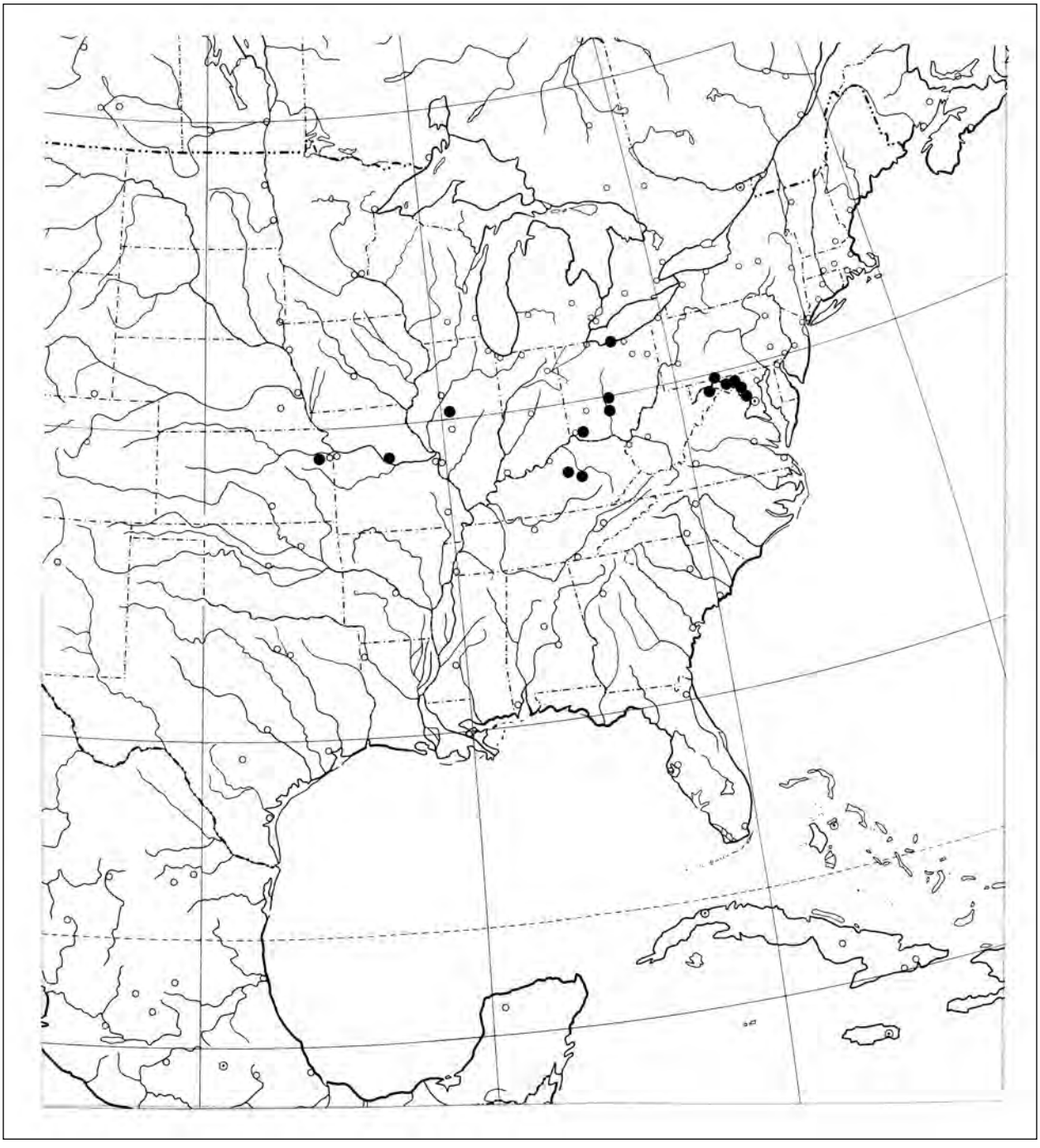
Map 12. Distribution of *Celticecis oviformis*.



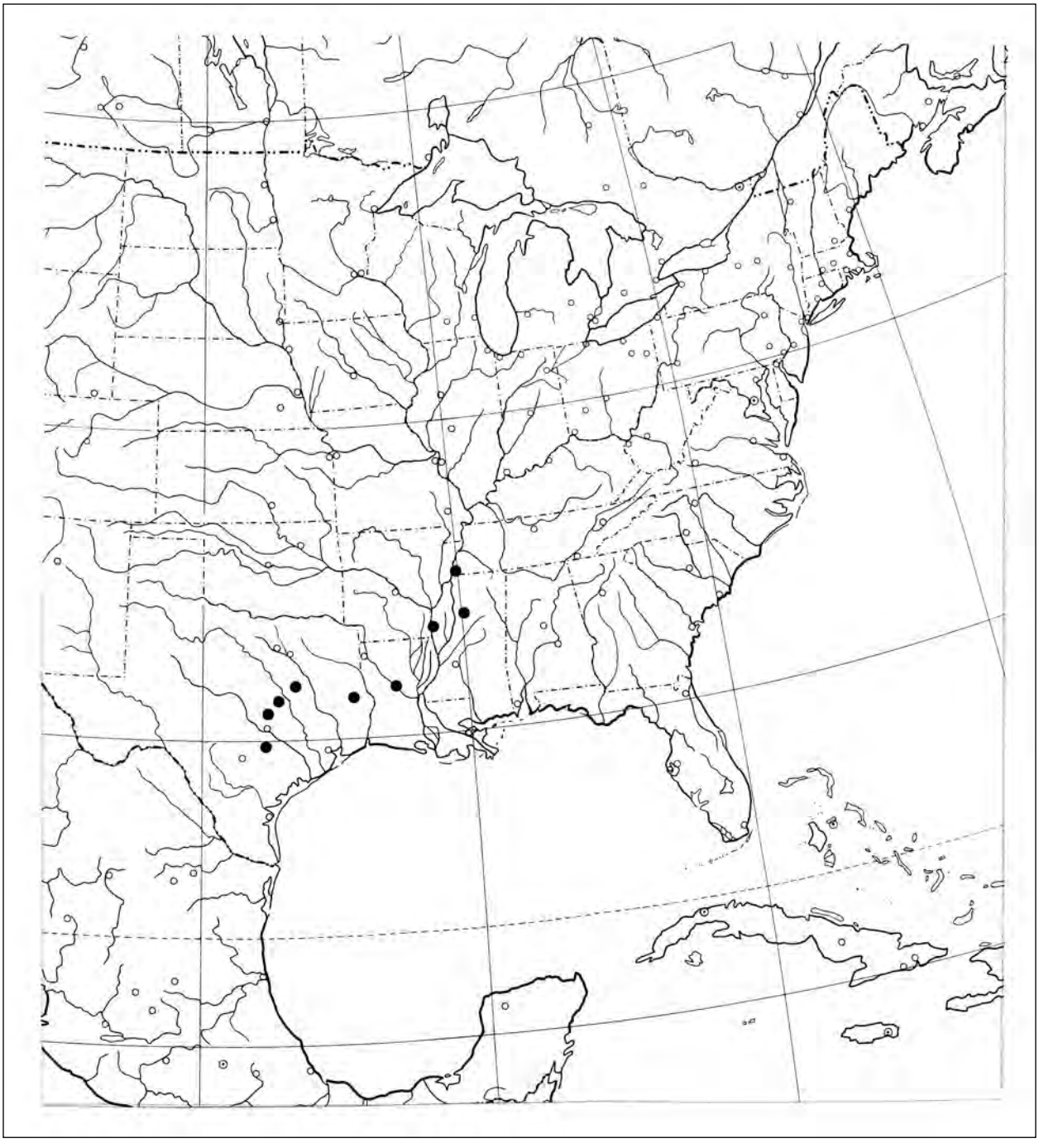
Map 13. Distribution of *Celticecis pilosa*.



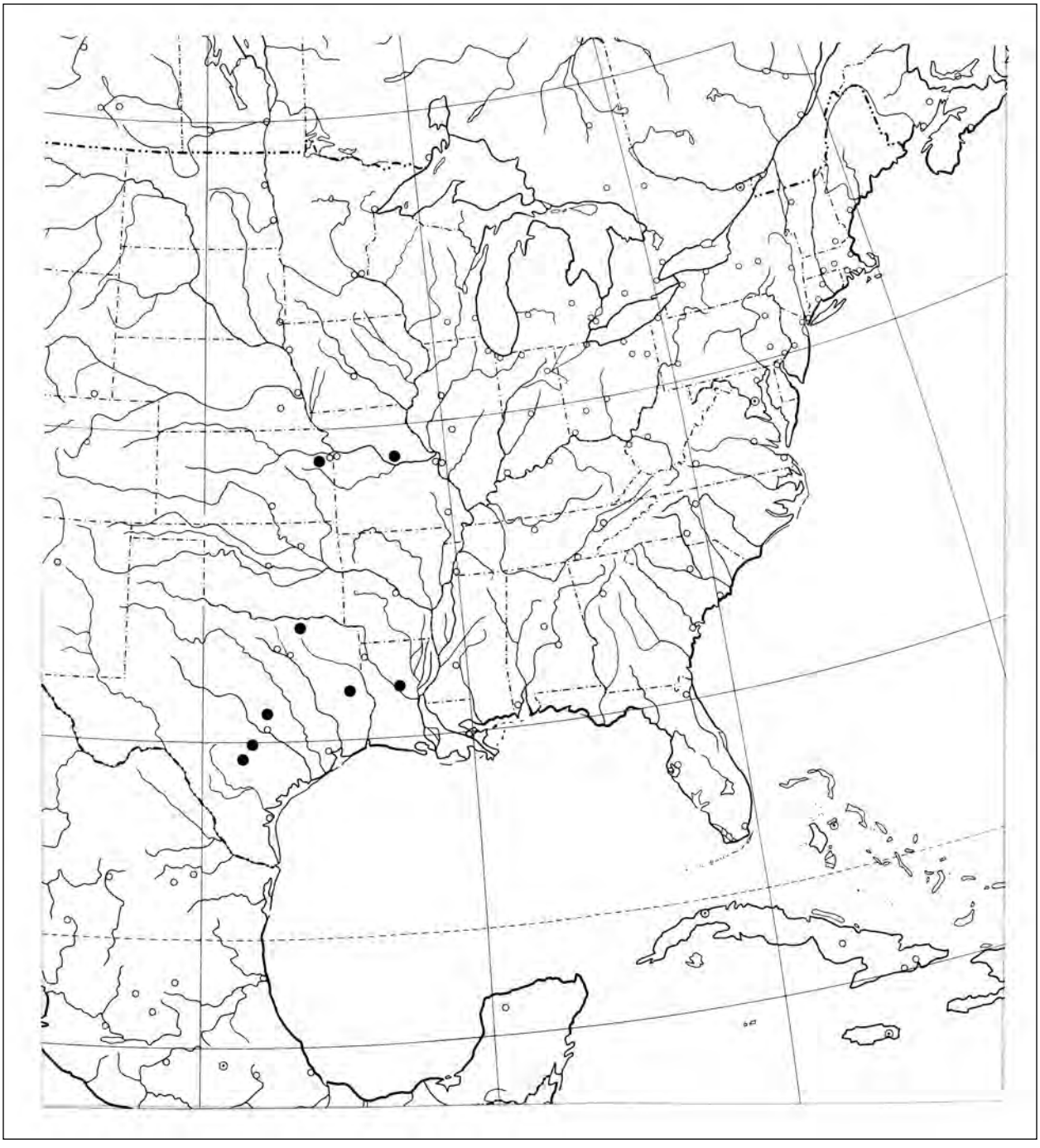
Map 14. Eastern North American distribution of *Celticecis pubescens*. It occurs also in Arizona.



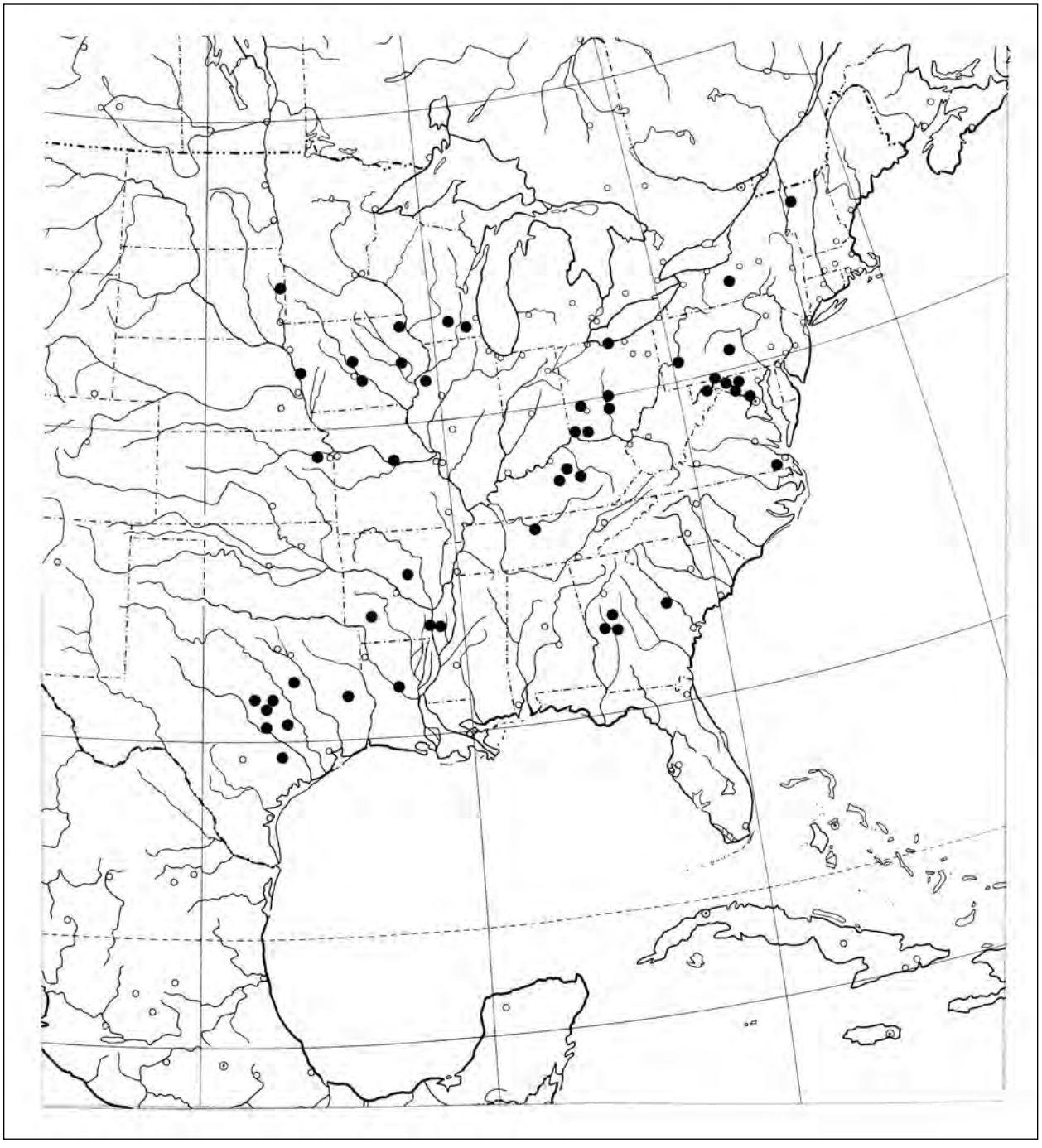
Map 15. Distribution of *Celticecis pyriformis*.



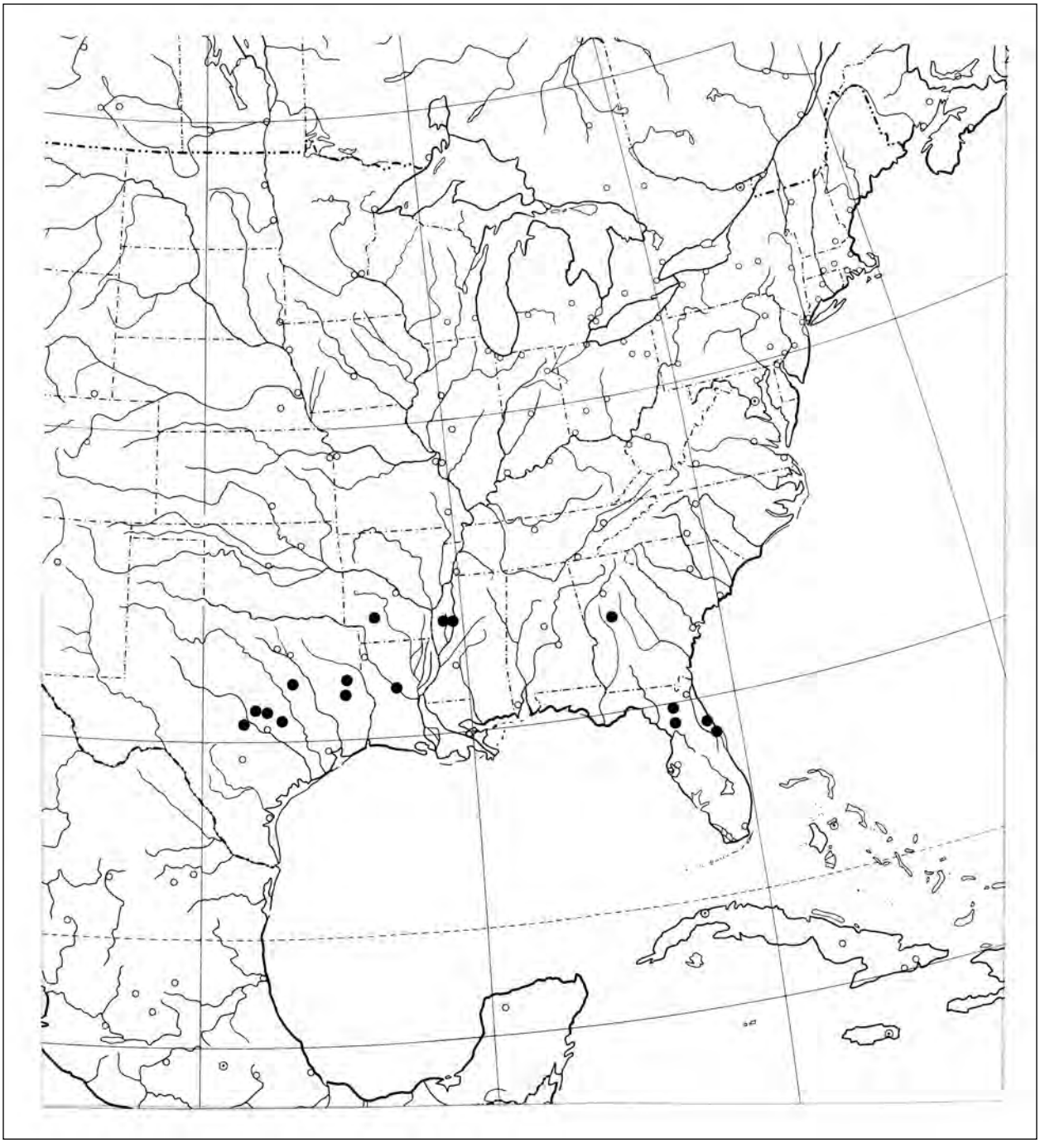
Map 16. Distribution of *Celticecis ramicola*.



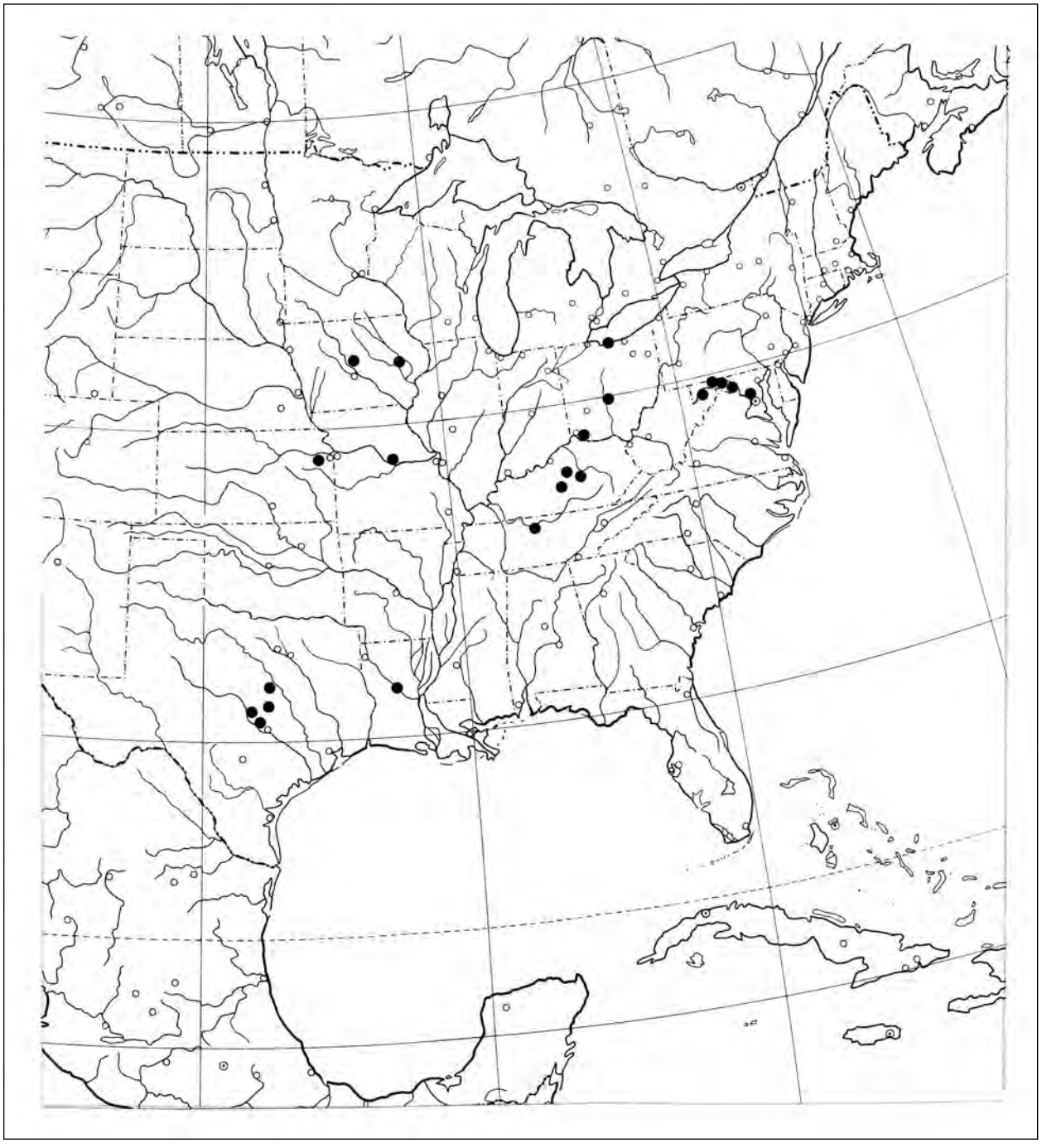
Map 17. Distribution of *Celticecis semenrumicis*.



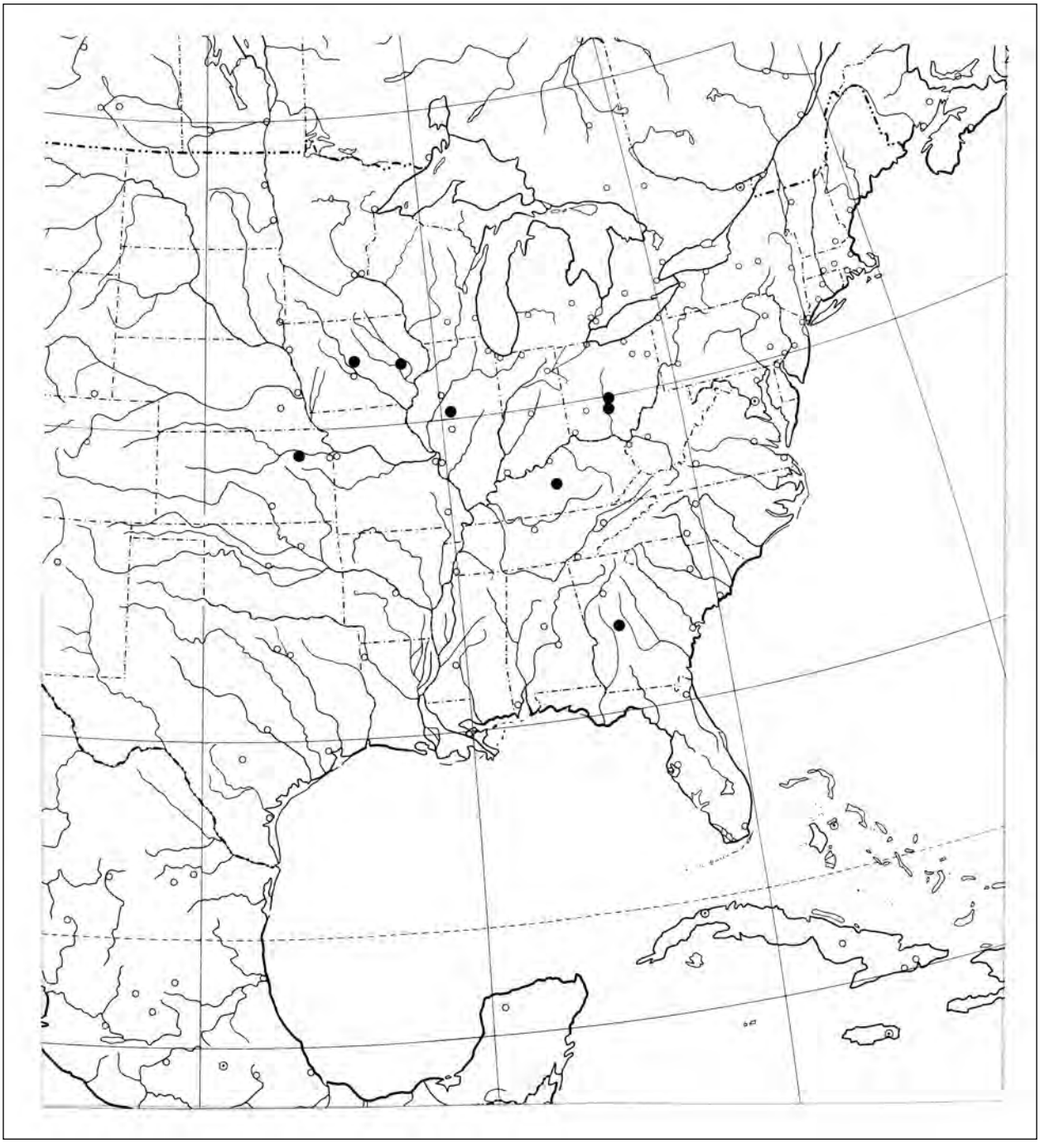
Map 18. Distribution of *Celticecis spiniformis*.



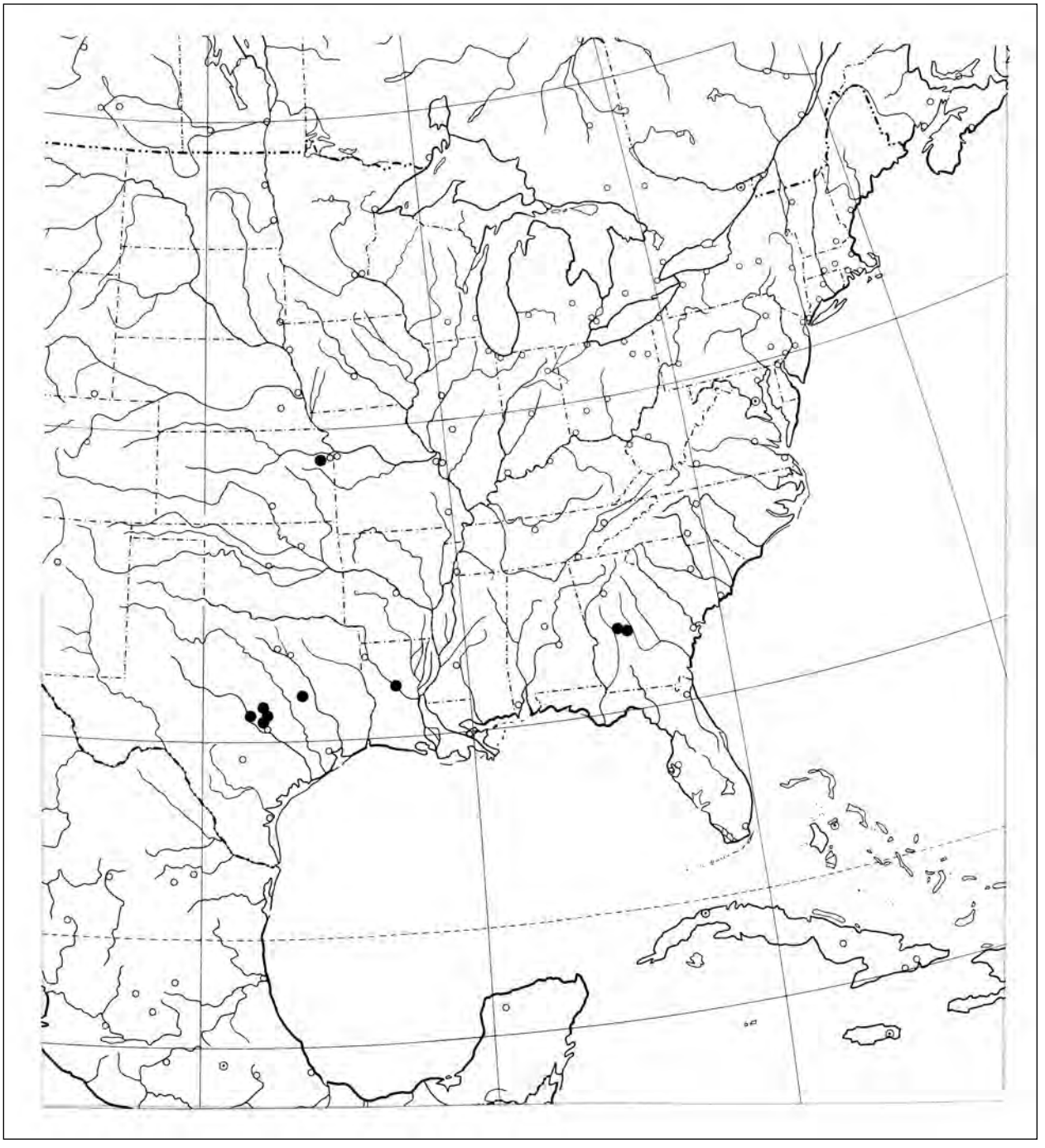
Map 19. Distribution of *Celticecis subulata*.



Map 20. Distribution of *Celticecis supina*.



Map 21. Distribution of *Celticecis wellsi*.



Map 22. Distribution of *Peracecis fugitiva*.